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Generic monograph of the Asteraceae-Anthemideae

KÅRE BREMER

Department of Systematic Botany, Uppsala University, Villavägen 6, S-752 36 Uppsala, Sweden

CHRISTOPHER JOHN HUMPHRIES

Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

Synopsis. The Asteraceae tribe Anthemideae is revised. In all, 12 subtribes, 108 genera and 1741 species are recognized; nine tribes are described as new and three, the Anthemidinae, the Artemiisinae and the Chrysanthemineae are emended in circumscription. Four new genera are described and many have been revised in circumscription. The definitions of the tribe, subtribes and genera are expressed in terms of sister group relations and the most robust hypotheses of character distribution utilizing the principles of synapomorphy, parsimony and character congruence. Phylogenetic relationships were determined using the tree-building computer program, HENNIG86. Cladograms of the subtribes and genera are provided together with a synoptic character analysis of each individual clade. A key to all genera is provided, each genus is described, all species currently recognized are listed with a brief synonomy and the relevant nomenclature and taxonomic changes are discussed in detail. Summaries of distributions are given in tables and within the generic accounts. The account ends with a list of excluded taxa and a taxonomic index.

INTRODUCTION

The Asteraceae tribe Anthemideae is one of the largest tribes of the family with 1741 species predominantly distributed in Eurasia, North and South Africa, with fewer species in North America and Australasia. The circumscription of the tribe is new but generally follows that outlined by Bentham in Bentham & Hooker (1873*a*).

The principal taxonomic problems within the tribe are almost entirely relationships between genera but also circumscription of genera especially within subtribal groups such as the Artemiisinae, the Chrysantheminae, and the 'Tanacetinae'. This revision deals with the systematics and generic circumscription of the Anthemideae utilizing modern cladistic methods. The nomenclature and descriptive taxonomy have been fully revised in line with our own analyses and the literature scanned up to the present time. In addition to the formal taxonomic treatment a complete description of character definitions, character distributions and morphologies has been provided. Phytogeography and phylogeny have been included to give the correct context for the novel classifications and a brief historical review of tribal and subtribal groupings is also presented.

MATERIALS AND METHODS

The revision is based on herbarium specimens and living collections in botanic gardens. The rationale was to study as many of the recognized species as possible during the course of the work. Those species which we have been unable to locate are indicated with an asterisk (*) in the individual lists at the end of each generic account. We have studied specimens from the following herbaria; (*Index Herbariorum*; abbreviations as in Holmgren et al, 1981) BM, BOL, BRY, E, F, GH, K, LE, M, MO, NBG, NY, PRE, S, US. Several species have been transferred during the course of the revision and new combinations are provided. For some North African species new combinations based on names in the unpublished thesis of Helen Wilcox are validated here.

The generic descriptions and the character matrices are based on dried herbarium specimens and living specimens when these were available. Cross-sections of cypselas were made from reconstituted collections, softened in water, embedded in paraffin and ceresin wax, cut by microtome and stained with safranin and light green. The material examined has not been listed but all specimens examined were of known provenance.

Descriptive terminology

The descriptions and terms used throughout this work follow those in Featherly (1954) and Stearn (1966). The terminology for outlines and plane shapes adopted is that of the Systematics Association Committee for Descriptive Biological Terminology (1962). Descriptions of variation in corolla morphology generally follow those of Jeffrey (1977).

Taxonomic concepts

The taxonomic concepts in this revision are based on morphological studies. In most generic revisions, particularly in large families such as the Asteraceae, genera and higher taxa are frequently circumscribed on uncritical character analyses. This approach is considered by us to be unacceptable since in no way does it reflect the principles of cladistics. Generic names, as with all taxa of any rank, can only be applied to monophyletic groups. To recognize monophyletic groups which can be designated as genera (or species, or tribes) the concept of resemblance has to be resolved so that hypotheses of characters can be used to generate hypotheses about groups. Evolutionary novelties or synapomorphies, are those characters which diagnose monophyletic groups and have been utilized here accordingly (see Humphries & Funk, 1984).

Cladistics

The technique we have used to diagnose monophyletic groups is the Wagner algorithm as implemented in the computer program Hennig86 (Farris, 1988). Hennig86 is an interactive program for cladistic analysis which can obtain most parsimonious trees by either exact or heuristic calculations. Characters were scored from the raw character matrices into discrete binary codes. Many of the characters we used were simply presence or absence characters and thus all characters were discretely coded in either a 0 or 1 state. However, a considerable number of the characters were polymorphic in their distribution especially in the larger genera. For precise details of the conventions adopted refer to the section on character coding. The character scores are presented in twelve matrices (Tables 4, 6, 8, 10, 12, 13, 15, 17, 19, 21, 23, and 25; see taxonomic accounts below); eleven are for individual subtribes (Anthemidineae is combined with the Chrysantheminae) and one for subtribes represented as individual taxa (Table 4). For the analysis of subtribes the matrix (Table 4) was analysed as presented. For the subtribe matrices there are three blocks of scores within each matrix; the first represents character distributions at a level higher than subtribe, the second is characters varying within the subtribe and the third provides a summary of ambiguous information for a given subtribe. Cladistic analysis for the subtribes is based on the central block of characters in each of the data matrices.

Trees were calculated using a variety of options in Hennig86. All four commands, and five of the nine tree building options available in Hennig86 were utilized depending upon the size and complexity of each data matrix. The options were as follows; *hennig* (h), which constructs one tree with one pass through the data; *mhennig** (mh*) which constructs several trees, each by a single pass, adding the terminal taxa in several different sequences. Branch swapping was applied to each of the initial trees and one tree from each initial one was retained in the memory; *branch-breaker** (bb*) a similar option to *mhennig** but all of the obtained equally parsimonious trees were retained, as was allowed in the assigned memory of 128k in the computer; *implicit enumeration* (ie*) which generated all possible shortest trees. The results guaranteed shortest trees and all equal length trees were retained in the available tree space; *ie-* which found one guaranteed shortest tree by implicit enumeration.

Exact analyses (implicit enumeration) were applied to the Achilleinae, Anthemidinae, Cancriniinae, Chrysantheminae, Gonosperminae, Handeliinae, Tanacetinae, Thaminophyllinae and the Ursiniinae. The *hennig*, *mhennig** and *bb** options were applied to the larger groups including the Anthemideae tribal analysis and the analyses of the Artemisiinae, Leucantheminae and Matricariinae subtribes. The trees were all rooted utilizing the outgroup – a taxon scored from a North American group of genera within the Heliantheae tribe. All scored characters in each of the matrices were given equal weight. Unknown scores were left in since Hennig86 has the facility for coping with them. In the cases where more than one equally parsimonious tree was obtained the *nelsen* command was activated to produce a strict consensus tree (Farris, 1988). However, for the purpose of the classification only one of the final trees is figured in the text (see Figs 1, 2, 7, 11, 17, 20, 23, 31, 36, 41, 47 and 51; see taxonomic text below). Each tree was diagnosed using the *xsteps* command in order to determine the states of the hypothetical ancestors on each tree (i.e. the node states) and to generate statistics on length and fit.

Precise details of character changes along each clade are provided in the subtribe accounts. Each cladogram is provided with a unique letter and number code and the length and consistency of each tree is provided in the figure caption. The cladograms should be used in conjunction with the descriptive accounts of the character changes.

Outgroup

Bremer (1987) has put forward evidence for the hypothesis that Anthemideae and Heliantheae sensu lato are sister groups within a larger clade consisting of the Calenduleae, the Senecioneae, the Anthemideae and the Heliantheae. Bremer also showed that the Anthemideae and its postulated relatives in the Heliantheae share similar ray floret epidermis as elucidated in the work of Baagøe (1977). The two tribes also have similar habit and foliage with trinerved and dissected leaves especially in the subtribe Helenieae, and thus the North American species of this group were selected as the outgroup. It has been pointed out to us by Charles Jeffrey (in litt.) that the results published by Palmer et al. (1988) from an analysis of chloroplast DNA would suggest that we might consider a different outgroup. The consensus tree of Palmer et al. using 926 restriction site mutations places Astereae and Anthemideae as sister groups and the Eupatorieae as an ingroup of the Heliantheae. However, we consider that their sample of taxa is so preliminary that for the time being we remain with Bremer's (1987) morphological hypothesis.

TRIBAL AND SUBTRIBAL DIVISIONS

The first coherent tribal classification of the Asteraceae was that of Cassini (1817, 1826) who recognized 19 tribes in the

family. The precise systematic position of the Anthemideae within the Asteraceae is shown in a diagram of the family when Cassini used a map with an oval arrangement of abutting circles to express the relationships of the tribes (King & Dawson, 1975). The Anthemideae were sandwiched between the Inuleae and the Ambrosineae. Cassini expressed the opinion that the Anthemideae are most closely related to the Heliantheae although in style structure they were very similar to the Inuleae, the Senecioneae and the Nassauvineae. Cassini (1826) divided the tribe into two major groups: Anthémidées – Prototypes (Anthemideae-Archetypae) and Anthémidées – Prototypes vraies, based on the prescence or absence of receptacular scales respectively. For many genera the division is quite workable and many of them can be placed in one group or the other. However, the artificiality of this character can clearly be demonstrated in several taxa especially the genus *Anthemis* (*Ammanthus* group) in which paleate and non-paleate forms can occur within one species (Heywood & Humphries, 1977).

Lessing (1832) had a quite different treatment from that of Cassini, and although his classification was avowedly artificial, since it was written with identification in mind, it clearly influenced the later major treatments of de Candolle (1837), Bentham (1873*a*, *b*), and Hoffmann (1894) (see Heywood & Humphries, 1977). Lessing recognized eight tribes and the genera of the Anthemideae were included in tribe VII Senecionideae subtribes Chrysanthemeae and Artemisieae. The Chrysanthemeae were further subdivided into two taxa of indefinite rank, the Anthemideae and Chrysanthemeae, and the Artemisieae were divided up into six taxa of indefinite rank.

De Candolle (1837) recognized Cassini's tribe Anthemideae as a subtribe and more or less followed Lessing's indefinite ranks which he categorized as divisions. However, he synonymised the Santolineae with the Euanthemideae. Bentham (1873a) recognized the Anthemideae as a tribe and divided it into six informal taxa. Four of these were common to the Lessing and de Candolle treatments but he also recognized the Lidbeckieae and the Tanaceteae as separate taxa. Of other 19th century works, that of Hoffmann (1894) is the only one of significance and he simply recognized the Cassini classification, dividing the tribe into two subtribes.

Baillon (1886) provided an end of century classification of the angiosperms in his classic *Histoire des plantes*. For the Asteraceae he recognized eight tribes and four hundred and three genera. The sub-series Anthemidées was included in an enlarged tribe Hélianthées together with the Héléniées, Sénécionées and the true Euhélianthées.

Most 20th century contributions have been concerned with the classification and delimitation of genera but rather silent about suprageneric classification and the relationship of the tribe to other tribes. However, Bessey (1915) provided perhaps the most novel treatment of the Asteraceae when he raised the family to the rank of order and raised fourteen tribes to family status. Family 296, the Anthemidaceae was sandwiched between families 295 and 297, the Eupatoriaceae and the Senecionidaceae respectively. However, most treatments have simply tended to follow the tribal groupings outlined by Bentham (1873*a*) with no real modifications to the status of infra-tribal groups (e.g. Carlquist, 1976; Cronquist, 1955, 1977; Wagenitz, 1976).

Poljakov (1967) recognized six subtribes in the Anthemideae in a treatment that to some extent resembled that of Bentham but with a more detailed consideration of the Artemisiinae.

One of the most recent attempts at creating subgroups within the tribe is that of Reitbrecht (1974) who considers that the Anthemideae consists of seven provisional groups (Humphries, 1979). These include the *Ursinia* group, to include *Ursinia* and its allies, the *Lasiospermum* group to include the majority of the African genera, especially *Lasiospermum* and *Eriocephalus*, the *Chrysanthemum* group for some members of the Tanacetinae, Chrysanthemineae and Leucanthemineae as recognized by us, the *Matricaria* group to include the Anthemidineae and some members of the Matricariinae, and the *Cotula* group for various other members of our Matricariinae.

Bremer (1987) undertook the first cladistic analysis of the tribes of the Asteraceae. The cladogram he obtained suggested a number of novel groupings. The Anthemideae were clearly placed in the monophyletic subfamily, Asteroideae, and appeared as the sister group of the Heliantheae in a subgroup consisting of the Calenduleae, the Senecioneae, the Anthemideae and the Heliantheae, with the Astereae and the Eupatorieae as sister groups. Bremer obtained his result by considering that the Anthemideae and the Heliantheae share similar ray floret cells (Baagøe, 1977), and similar foliage with trinerved and dissected leaves which are interpreted as synapomorphies for the two tribes.

Some of the older groups recognized by the 19th century authors have caused problems as a result of different interpretations of characters considered of importance in classification. One of the most problematic groups within the Anthemideae is the *Ursinia* group, and *Ursinia* in particular. *Ursinia* resembles the Anthemideae in habit and the Arctotideae in terms of superficial features of the capitulum. The interpretation as to its exact position has varied, depending mostly on the weight of individual characters rather than any form of character analysis. Bentham (1873*a*) placed *Ursinia* in the tribe Arctotideae (sensu Norlindh, 1977) mainly because of its well developed pappus scales. Cassini (1816) followed by Beauverd (1915), Merxmuller (1954), Prassler (1967), and Reitbrecht (1974) considered it to be a member of Anthemideae. Robinson & Brettell (1973) argued that the inclusion in the Anthemideae of an anomalous genus like *Ursinia* with its conspicuous pappus scales, widely ovate apical anther appendages, and different pollen morphology (exine without columnar structure) stretched the workable tribal concept. They proposed a new tribe, Ursinieae, which included only *Ursinia*. However, they were not working within a cladistic framework and have used in our opinion autapomorphic characters to define their new tribe. Acceptance of their solution does nothing to actually clarify the position of the Ursinieae in terms of its sister group relations and would render the Anthemideae as paraphyletic if the Ursinieae were excluded from it. As described in the generic account, we consider the large pappus scales and the shape of the apical anther appendage plesiomorphic within the Anthemideae, since similar structures occur in the outgroup. The pollen was investigated by Stix (1960) and she concluded that *Ursinia* belongs to the Anthemideae. The presence of unique furanosesquiterpenes which must be considered as apomorphic for *Ursinia* and other South African genera of the subtribe Ursiniineae, in our view diagnoses the Ursinieae as a natural group and corroborates its tribal position as a member group of the Anthemideae.

Bentham's informal group, the Cotuleae, has also been

scrutinized by a variety of workers in recent years. Bentham (1873*b*) recognized the 'Cotuleae' mostly by 'the mutual possession of characters representing loss or reduction in the habit and various parts – involucre, paleae, ray florets, pappus, number of corolla teeth and stamens (to four) and seed-sterility of disk florets' (Lloyd, 1972*a*). It is a classic polyphyletic group and all of its constituent members (12 genera; Table 1) have been analysed in terms of gross morphology (Heywood & Humphries, 1977), flower and fruit structure (Bruhl & Quinn, 1990, 1991), and pollen morphology (Jarvis, 1976; Bruhl & Quinn, 1991). Most of the taxa of the Cotuleae are very small plants occurring in the southern hemisphere with structurally reduced parts. The detailed morphological analyses have shown that most taxa are misplaced within the Anthemideae and these are marked with asterisks in Table 1. Several of these have already been transferred to other tribes (see list of excluded genera, Heywood & Humphries, 1977). The remainder are all members of our revised group, the Matricariinae, in which *Cotula*, *Leptinella*, and *Soliva* are all closely related genera.

In addition to those studies listed by Heywood & Humphries (1977), in recent years there have been several studies of higher classification in the Anthemideae, particularly by Swedish workers within the Museum of Natural History, but these have concentrated on taxa selected within the tribe. For example, Nordenstam (1976*a*) reclassified a number of genera masquerading under the name of *Chrysanthemum* in South Africa and Källersjö (1988) examined the patterns of relationship in the South African *Pentzia* group of genera.

CLASSIFICATION

Subtribal classification

In this study an entirely new subtribal classification is proposed. We have grouped genera into larger monophyletic entities, subtribes, rather than by a more traditional method of dividing the tribe using particular characters. We are fairly confident that we have identified a number of monophyletic entities, and produced a number of well supported cladograms. At this time we find it appropriate to recognize 12 subtribes, most of which represent generic groups that are fairly well understood as monophyletic. Several peculiar genera of uncertain position have been more or less provisionally accommodated in otherwise homogenous subtribes.

Table 1 The 'Cotuleae' group as recognized by Bruhl & Quinn (1990, 1991).

1	*Abrotanella* *
2	*Centipeda* *
3	*Ceratogyne* *
4	*Cotula*
5	*Dimorphocoma* *
6	*Elachanthus* *
7	*Isoetopsis* *
8	*Leptinella*
9	*Nananthea*
10	*Plagiocheilus* *
11	*Soliva*
12	*Tripleurospermum*

* = excluded genera

We think it is better to present a hypothesis on the relationships of such genera of uncertain position rather than simply listing them at the end of the tribe. However, genera excluded from the Anthemideae are simply listed at the end of the revision.

The predominantly Asian subtribe 'Tanacetinae' is only a provisional taxon in this treatment. It is at best paraphyletic and will probably turn out to be polyphyletic in later studies. It contains the large genus *Tanacetum*, a dubious taxon of critical importance in future studies of the Anthemideae. In our study we have grouped together a number of genera that appear to have their sister groups within *Tanacetum*. Furthermore, it is possible that several other subtribes also have their sister groups within *Tanacetum*. It is clear to us that the subtribe 'Tanacetinae', and most particularly *Tanacetum* itself, are unresolved taxa.

Ursiniinae, Gonosperminae, Handeliinae, Chrysantheminae and Thaminophyllinae are homogeneous and monophyletic subtribes without inclusion of problematic genera. Some generic affinities within these subtribes have been understood by earlier authors, but in general they are emended here. For example, the Canary Island *Lugoa* and *Gonospermum*, a well known generic pair, are associated with the South African *Inulanthera*, and the three genera form our subtribe Gonosperminae.

Ursiniinae is the South African group containing furanosesquiterpenes (Greger, 1977, and references therein) and the precise delimitation of the Ursiniinae was undertaken by Källersjö (1986).

Handeliinae contains a number of small Asian genera. The association of *Sclerorhachis* with the other genera of the Handeliinae is new. The affinities between the other genera are described already by Tzvelev (in Komarov, 1961) although he did not recognize the subtribe and he placed them in widely different positions in his floristic classification.

Chrysantheminae as we understand it is a small group that has been identified by earlier authors (see Humphries, 1976; Heywood & Humphries, 1977, and references therein).

Thaminophyllinae is a South African subtribe that hitherto has hardly been considered, although affinities of some genera have been discussed by recent authors (Nordenstam, 1976; Bond, 1980).

Cancriniinae, Artemisiinae, Achilleinae, Anthemidinae, Leucantheminae and Matricariinae are subtribes that we also consider monophyletic with the character information used in this study. Further investigations may result in changes in their delimitation, however, since a number of problematic genera are involved and the defining characters are rather few in some subtribes. Affinities between several of the genera within each of these subtribes have been indicated by earlier authors but their precise delimitations here are entirely new.

The Asian Cancriniinae seems homogeneous but may eventually become a larger group, as its relatives probably occur within the undefined subtribe 'Tanacetinae'. The affinities between some of the genera of the Cancriniinae have also been described by Tzvelev (in Komarov, 1961).

The mainly Asian and large subtribe Artemisiinae contains the *Artemisia* group of genera, an assemblage that has been recognized for some time (e.g. Besser, 1829). We have added their plesiomorphic relatives to this group. The relationships of some of these genera to *Artemisia* and its relatives have been indicated by Poljakov (1955) and Tzvelev in Komarov (1961).

The Eurasian/North African subtribe Achilleinae is a generic group hitherto unrecognized. Interrelationships between a few of the genera have been understood (e.g. *Achillea*, *Anacyclus*, and *Leucocyclus*, Humphries, 1979; Greger, 1977; Valant-Vetschera, 1981) but the subtribe is a new generic grouping. *Santolina* is a plesiomorphic genus of uncertain position. It may have close relatives within the 'Tanacetinae'.

In this treatment the Anthemidinae contains only two genera: *Anthemis* and *Nananthea*, the latter a specialized genus of uncertain position, and discussed at greater length in the generic account.

The predominantly Mediterranean Leucantheminae includes a large subgroup, the *Leucanthemum* group, which has been largely elucidated by the studies of Wilcox (1977) and is considered by us to be a well supported monophyletic unit. *Leucanthemopsis* is generally associated with *Leucanthemum* (Heywood, 1954, 1976) and to it we add *Phalacrocarpum*, *Hymenostemma* and *Prolongoa*. There are other small genera of more uncertain position, such as *Lepidophorum*, *Nipponanthemum*, *Leucanthemella* and *Nivellea*. Pending further studies, we have considered it worthwhile to include them in the Leucantheminae.

The large cosmopolitan subtribe, Matricariinae, represents one of the more interesting generic groupings presented in this study. We consider it monophyletic with reservations for a few genera of possible uncertain position such as *Rennera* and *Oncosiphon*. Within the Matricariinae there is the southern hemisphere *Cotula* group, an homogeneous, monophyletic unit, quite distinct from the generic assemblages introduced by Bentham (1873*a*) and discussed by more recent authors (see e.g. Heywood & Humphries, 1977; Bruhl & Quinn, 1990, 1991). We have refrained from recognizing the *Cotula* group as a subtribe, since it would probably make the remaining Matricariinae paraphyletic. Related to the *Cotula* group are several predominantly Mediterranean and South African genera, the interrelationships of which have hitherto been unprescribed.

Although we feel that the majority of our subtribes are well supported and easily distinguished, subtribal interrelationships have been difficult to assess and the main cladogram (Fig. 1) is largely unresolved at the subtribal level. The cladogram as presented is one of several equally parsimonious hypotheses. We suggest that the Ursiniinae and Cancriniinae are plesiomorphic particularly in terms of the scale-like pappus structures as compared to other tribes. The genus *Ursinia* within the subtribe Ursiniinae has always been considered to occupy an anomalous position in the Anthemideae. In our opinion, this is partly due to the presence of plesiomorphic features. Some of these, particularly basal arrangements of leaves and basal woodiness and the internal anatomy of cypselas in some members of the Ursiniinae and other relatively basal taxa such as the Cancriniinae, are remarkably similar to those found in members of the outgroup which we interpret as examples of symplesiomorphy.

Within the remaining group of ten subtribes it is reasonable to suggest that the predominantly Mediterranean and South African subtribes, such as the Achilleinae, Anthemidinae, Chrysantheminae, Leucantheminae, Thaminophyllinae and Matricariinae are closely related to each other because of shared possession of floral resin canals as compared to the mainly Asian 'Tanacetinae', Gonosperminae (African but apparently directly related to *Tanacetum*), Handeliinae and Artemisiinae. We admit that such a character is vague in circumscription but we offer this classification as a basis for further investigation. The Thaminophyllinae and Leucantheminae may be closely related subtribes because of similarities in foliage characters.

Generic classification

At the generic level a number of changes should be noted. The status of particular genera as being monophyletic or non-monophyletic will be discussed briefly. We have adopted a conservative style and undertaken generic redelimitations only whenever necessary and wherever possible. Our aim has been to reclassify para- or polyphyletic genera and maximize the number of monophyletic genera within the Anthemideae. In many cases we have been content in discussing the non-monophyletic status of existing genera, to leave redelimitations of ambiguous taxa to future systematists.

Many of the new and redefined genera have been analysed in more detail and considered by authors working in close connection with us (Källersjö, 1986, 1988, 1991; Bremer & Källersjö, 1986; Nordenstam, 1976; Ling, 1980*a*, *b*, 1991*a*, *b*; Wilcox, 1977). The definitions and dispositions of these new genera as determined by these authors include *Inulanthera* (Gonosperminae), *Rhodanthemum* (Leucantheminae), *Oncosiphon*, *Myxopappus*, *Foveolina* and *Hilliardia* (Matricariinae) and *Seriphidium* (Artemisiinae). Redefined genera include *Phymaspermum*, *Hymenolepis*, *Athanasia* (Ursiniinae), and *Pentzia* and *Rennera* (Matricariinae).

New genera described within this monograph include *Chrysanthoglossum*, *Nivellea*, *Leucoglossum*, and *Rhodanthemum*, taxa all within the Leucantheminae. *Richteria* (Cancriniinae) and *Ismelia* (Chrysantheminae) are two small genera originally described during the 19th century, later reduced into synonomy and then re-established here. Typically misplaced species have been transferred to a variety of genera such as *Microcephala* and *Aaronsohnia* (Matricariinae). Also, it should be noted that taxonomic changes established here have dramatically improved the delimitation and definitions of well-known genera such as *Artemisia*, *Chrysanthemum* (s.s.), *Leucanthemum* and *Tripleurospermum*. By removing a number of species from these formerly non-monophyletic genera and assigning the misplaced species to new genera, the streamlined versions of the new taxa are now more likely to be monophyletic.

The majority of genera within the Anthemideae are monophyletic taxa but there are several exceptions which will obviously require further taxonomic work, as indicated in further detail in the generic accounts. Of the relatively smaller taxa, genera without autapomorphies include *Eumorphia* (Ursiniinae), *Richteria* (Cancriniinae), *Tanacetopsis* ('Tanacetinae'), *Gonospermum* (Gonosperminae), *Sphaeromeria* (Artemisiinae), *Mecomischus* and *Chamaemelum* (Achilleinae), *Leucanthemopsis* and *Coleostephus* (Leucantheminae), and *Cymbopappus* and presumably *Matricaria* (Matricariinae). Future work should reveal whether they are monophyletic or non-monophyletic taxa. Amongst the larger genera, *Achillea* is one of similar uncertain stature.

Tanacetum ('Tanacetinae'), *Dendranthema*, *Ajania* and *Artemisia* (Artemisiinae), and *Cotula* (Matricariinae) are shown to be non-monophyletic. Other genera and even groups of genera have their sister groups within these taxa and eventually they will have to be split into smaller monophyletic units. In the next few years we envisage further changes of considerable magnitude which will necessitate

taxonomic and nomenclatural rearrangements quite different from those traditionally recognized.

CHARACTERS OF THE ANTHEMIDEAE

The characters used in the cladogram and for delimitation of genera are discussed below (see Table 2). The terms character and apomorphy are used synonymously, since any character is apomorphic at its universal level within the taxonomic hierarchy. The corresponding plesiomorphic condition is omitted from the character table. In obvious cases, such as perennial being considered as plesiomorphic as compared to annual, the perennial condition is not mentioned. In other characters the corresponding plesiomorphic conditions are explained elsewhere. The identification of characters and character states was undertaken by outgroup comparison with parts of the Asteraceae-Heliantheae.

Character scoring

There have been problems in scoring character states. For several character states, particular variables are expressed only within some species of a particular genus. Furthermore, the problem of unknown or inapplicable character states has caused conflicts during analysis. As far as this study is concerned each character may be scored in one of five different ways for a particular genus:

1: The character is present in all species of the genus.

a: The character is polymorphic and present in only some but not necessarily all species of the genus. We take the line that all characters of this type are originally present within a genus but secondarily lost in some species. This interpretation is based on comparison with the immediate relatives of the genus, identified during or after cladistic analysis. If the character is present in the sister taxa or close relatives, it is also considered originally present within the genus; 'a' stands for apomorphic. This method is simply outgroup comparison with the ingroup restricted to a particular genus being scored for the character.

0: The character is absent from all species of the genus.

p: The character is absent from some but not necessarily most species of the genus. It is interpreted as originally absent within the genus; 'p' stands for plesiomorphic but independently derived in other species. The reason for this interpretation is similar to 'a' above. If the character is absent in the relatives, it is also considered originally absent within the genus.

?: The character is unknown or inapplicable to the genus. Characters relating to chemistry, embryology and chromosome number are sporadic and unknown for many genera. Other characters are inapplicable to some genera. For example, characters of receptacular paleae and ray florets are inapplicable in epaleate and non-radiate genera, respectively. In the cladograms (Figs 1–12; see taxonomic text below) unknown or inapplicable characters are assumed to be present or absent following the principle of parsimony. If the character is known to be present in some genera of a particular group, it is also considered present in all genera of that group, and vice versa.

Table 2 Characters used in the cladograms.

1 Plants annual.
2 Plants shrubby.
3 Plants spiny.
4 Plants compact and more or less scaphoid.
5 Plants with one or few sparsely branched stems arising from a woody villous caudex.
6 Plants rhizomatous with rosulate, spathulate-obovate-linear leaves.
7 Plants with branches in whorls below the first capitula.
8 Plants basally villous-tomentose with rather thick stems and a soft pith.
9 Plants covered with a dense greyish-white indumentum.
10 Plants covered with viscid hairs.
11 Plants with dolabriform hairs.
12 Plants with stellate hairs.
13 Plants with interxylary cork.
14 Leaves opposite.
15 Leaves variously deeply lobed or divided.
16 Leaves much pinnatisect with filiform lobes.
17 Leaves pectinate-pinnatisect with filiform, apically somewhat swollen and mucronulate lobes.
18 Leaves with few, oblong to rounded, apically mucronate lobes.
19 Leaves large with many rounded lobes.
20 Leaves spathulate in outline, ternate to ternately pinnate.
21 Leaves serrate-dentate.
22 Leaves entire or apically tridentate.
23 Leaves entire, ericoid.
24 Leaves rather fleshy, few-lobed or entire.
25 Leaves rather fleshy, entire, linear.
26 Leaves closely set, lanceolate to linear.
27 Leaves vermiform.
28 Leaves with secretory cavities.
29 Capitula densely corymbose.
30 Capitula very small and numerous in a large, dense, semiglobose corymb.
31 Capitula in a long narrow panicle or raceme.
32 Capitula in glomerules arranged in long spikes.
33 Capitula on short and nodding peduncles.
34 Capitula sessile along the stems.
35 Capitula discoid.
36 Capitula disciform.
37 Involucre rather narrowly urceolate.
38 Involucral bracts in 4–7 rows.
39 Involucral bracts in 1–2 rows, rather wide.
40 Involucral bracts in 2 unequal series.
41 Involucral bracts wide, flabelliform.
42 Involucral bracts subulate.
43 Involucral bracts with scarious margins.
44 Involucral bracts with dark brown margins.
45 Receptacle paleate.
46 Receptacle narrowly conical to subulate.
47 Receptacle hollow.
48 Receptacle pilose.
49 Receptacle densely hirsute.
50 Receptacular paleae pilose.
51 Floral parts with resin canals.
52 Ray floret limb white.
53 Ray floret limb golden yellow.
54 Ray floret limb bluish violet.
55 Ray floret limb deeply emarginate.
56 Ray floret limb epidermis cells tabular (senecioid or mutisioid type).
57 Ray floret tube sinus extending to the base.
58 Ray and disc floret tube dorsiventrally flattened.
59 Ray floret tube and cypsela pilose laterally; ray floret limb pilose abaxially.
60 Ray floret tube confluent with the cypsela.
61 Ray floret tube persistent on the cypsela.
62 Outer florets stalked.
63 Outer female florets in several rows.
64 Outer female florets subtended by scaphoid bracts.

Table 2 *cont*

65 Outer female floret corollas 'flask-shaped', tapering above or narrowly cylindrical.
66 Outer female floret corollas without teeth.
67 Outer female florets without corollas.
68 Outer female floret style-branches lanceolate, flat, acute.
69 Corolla gradually expanded, rather thin and funnel-shaped.
70 Corolla inflated with a hollow space between outer surface and inner layer.
71 Corolla apically contracted.
72 Disc corolla 4-lobed.
73 Disc corolla lobes with dorsal appendages.
74 Corollas with continuous veins extending into the lobes.
75 Disc corolla lobes with central resin sacs.
76 Disc corolla zygomorphic with 2 smaller adaxial lobes with marginal resin canals extending from the base of the corolla and with 3 larger abaxial lobes.
77 Disc corolla red.
78 Corolla apically with erect, straight hairs.
79 Corolla apically with long, reddish hairs.
80 Corolla apically with stellate hairs.
81 Corolla cobwebby pilose.
82 Disc corolla tube thickened in fruit.
83 Disc corolla tube very thick and brittle.
84 Disc corolla tube basally saccate at least adaxially.
85 Disc corolla tube deeply and equally saccate both abaxially and adaxially.
86 Corolla tube basally copiously swollen and spongy, almost enclosing the cypsela especially laterally.
87 Disc corolla tube confluent with the cypsela.
88 Disc corolla tube pilose.
89 Corolla tube with long-stalked glands; stalk cells elongated.
90 Disc corolla tube and cypsela ribs with thick vascular strands.
91 Central florets of two kinds; outer perfect, inner completely sterile with reduced ovaries.
92 Anthers caudate.
93 Anthers with triangular-linear-lanceolate apical appendages, of rather thick-walled cells.
94 Anthers with an apical resin sac.
95 Anthers with endothecial tissue partly or wholly polarized.
96 Pollen grains with short or without spines.
97 Pollen grains without spines.
98 Pollen grains hexa-panto-colporate.
99 Style slender, parallel-sided at base.
100 Style immersed in a lobed nectary.
101 Style persistent and spinescent in fruit.
102 Style-branches brownish.
103 Disc floret style-branches long-penicillate.
104 Disc floret style-branches fused.
105 Stylopodium large and persistent in fruit.
106 Central floret ovaries reduced; florets functionally male.
107 Cypselas terete to weakly angled, or flattened.
108 Cypselas turbinate.
109 Cypselas arcuate.
110 Cypselas ellipsoid, small, *c.* 1 mm long.
111 Cypselas subglobose, with 2–3 very thin lateral-adaxial ribs.
112 Cypselas large, with 3 thick protruding sclerenchymatous ribs, somewhat winged in ray cypselas.
113 Cypselas slender and tuberculate with numerous obtuse excrescences.
114 Cypselas dorsiventrally flattened.
115 Ray cypselas dorsiventrally flattened with 3 adaxial ribs.
116 Disc cypselas laterally flattened.
117 Cypselas laterally winged.
118 Ray cypselas laterally winged; wings projected to apical teeth.
119 Cypselas with sclerenchymatic lateral wings.
120 Cypselas heteromorphic; ray cypselas triquetrous, winged; disc cypselas terete to prismatic to laterally flattened.
121 Disc cypselas abaxially and adaxially winged.
122 Cypsela wings as apical spines.
123 Cypselas with a mainly abaxial entire or toothed rim.
124 Cypselas with 10 (8–12) multicellular epicarpic ribs.
125 Cypsela ribs basally fused into a more or less well developed foot callus.
126 Cypsela ribs protruding, narrow and somewhat wing-like.

Table 2 *cont*

127 Cypselas with 5 mainly adaxially arranged ribs.
128 Cypselas with 1 abaxial and 2 lateral thick ribs and 2–3 adaxial ribs.
129 Cypselas with 1 adaxial and 2 lateral rather thick ribs.
130 Cypselas with 2 lateral vascular strands, sometimes also with 1 adaxial strand.
131 Cypselas 10-ribbed with costal veins and resin canals.
132 Cypsela ribs with ellipsoid secretory cavities forming longitudinal ducts.
133 Cypselas with costal resin canals or sacs.
134 Cypselas with vallecular secretory canals.
135 Cypselas with vallecular vascular strands.
136 Cypselas abaxially and apically with 2 distinct, occasionally 1 or 3–5, resin sacs.
137 Cypselas with a single resin sac apically in the adaxial rib.
138 Cypselas with scattered elongated resin sacs.
139 Cypselas completely covered with rows of myxogenic cells.
140 Cypselas with myxogenic cells on abaxial surface and on the ribs of the adaxial surface.
141 Cypselas with dense rows of myxogenic cells also on the corona.
142 Cypselas with large myxogenic cells in rounded, scattered groups.
143 Cypselas with myxogenic cells in 2 distinct adaxial-lateral rows.
144 Cypselas with scattered, ovoid, myxogenic trichomes.
145 Cypselas papillose.
146 Cypselas long-papillose, seemingly pubescent.
147 Cypselas densely pilose; hairs subulate, with a few basal cells and one long apical cell.
148 Cypselas cobwebby pilose.
149 Cypselas with rather stiff unbranched hairs of 3–8 cells with spiral wall thickenings.
150 Cypselas copiously villous, seemingly covered in 'cotton wool'.
151 Cypsela wall without carbonized layer.
152 Cypsela wall several cell layers thick, partially or completely sclerified.
153 Cypsela thick-walled and conspicuously rugose.
154 Cypselas thin-walled, obovoid to oblanceolate, devoid of ribs.
155 Cypsela wall very thin, translucent and showing brownish black, rounded, very thick-walled testa epidermis cells.
156 Cypsela wall white and spongy; pericarpic cells isodiametric with thin spiral wall thickenings.
157 Cypsela wall with rod-shaped crystals in small packets.
158 Cypsela wall with numerous druses in the pericarp.
159 Cypsela wall with a continuous ring of fibre-like cells.
160 Cypsela wall with a continuous ring of sclerified isodiametric cells.
161 Pappus of short (not large and obovate or bristle-like) scales, an auricle, a corona, or absent.
162 Pappus of scales or teeth projected from the ribs.
163 Pappus of separate, mainly abaxial, subulate scales.
164 Pappus of 5 convolute-contorted scales.
165 Pappus a scarious, flimsy corona.
166 Pappus adaxially long.
167 Pappus a stiff adaxial auricle.
168 Pappus a large, scarious, adaxial but basally coroniform auricle, as long as the corolla or longer.
169 Pappus a large, scarious, adaxial, flabelliform auricle, as long as the corolla or longer.
170 Pappus scales brownish.
171 Pappus absent in disc cypselas, but present in ray cypselas.
172 Pappus absent in ray and disc cypselas.
173 Testa epidermis cells spirally arranged around the embryo.
174 Testa epidermis cells thick-walled and dark reddish.
175 Embryo sac tetrasporic.
176 Embryo sac disporic.
177 Chromosome number x=10.
178 'Irregular' monoterpenes in high concentrations present.
179 Furanosesquiterpenes present.
180 Particular thiophene derivatives present.
181 Amides present.
182 Flavonol 5-glucosides present.
183 Dehydrofalcarinone and dehydrofalcarinol present.
184 Anthocyanin present in root tips.

Habit

The outgroup comprises perennial herbs or half-shrubs, as in many Anthemideae. Throughout the tribe there are scattered annual genera, groups of genera or odd annual species or groups of species within otherwise perennial genera. The annual habit (character 1) is independently derived several times within the Anthemideae. The same holds for the shrubby habit (2), although this condition is less common within the tribe. No species of the Anthemideae grows into a tree. Other uncommon habit characters absent in the outgroup include characters 3–8.

Indumentum

The indumentum of the frequently pubescent Anthemideae commonly consists of unbranched hairs with a few basal stalk cells and a long apical cell. The same type is found in the outgroup and in many other Asteraceae. Occasionally in Anthemideae the hairs form a dense, tomentose to villous, greyish-white indumentum (character 9). In several Anthemideae dolabriform hairs are present (11) comprised of a stalk with few cells and transversely arranged apical cells, so that the hairs are T-shaped or Y-shaped. A distinction between T-shaped and Y-shaped hairs was made by Napp-Zinn & Eble (1980) but we find it difficult to maintain this distinction. Both types may be present, sometimes mixed together with intermediates. Dolabriform hairs are absent from the outgroup.

In a few genera stellate hairs are present (12), possibly derived from the dolabriform hairs. The stellate hairs also have a stalk of a few cells, but a stellate apical cell. The type is absent from the outgroup.

Glands composed of two parallel rows of cells with the apical pair enlarged are frequent in the Anthemideae, the outgroup and other Asteraceae. The number of cell pairs in the stalk varies, and at first sight there seem to be two types: one with several cells forming a stalk and one with a basal cell pair and an apical enlarged pair forming a sessile gland (cf. for example, Nordenstam, 1976). There are intermediates with two or more basal cell pairs, and hence we find it difficult to separate the two types into separate character states. Thus, we have avoided using any of them as a character. Occasionally, the viscid glands form a dense cover on the plant (10).

Wood anatomy

In Anthemideae-Artemisiinae a number of genera are provided with interxylary cork (character 13; Holmgren et al., 1976; Moss, 1940). Many genera have not been investigated. As far as we know it does not occur in the outgroup.

Foliage

In the majority of the Heliantheae the leaves are opposite. The outgroup of the Anthemideae within Heliantheae and the majority of Anthemideae have alternate leaves. This condition then seems best interpreted as a synapomorphy for the Anthemideae and part of Heliantheae, whereas the secondarily opposite leaf arrangement (character 14) is a character within the Anthemideae.

Variously dissected leaves are characteristic of most Anthemideae and entire leaves are rather rare exceptions. Dissected leaves also characterize the outgroup, and appear to be a synapomorphy (character 15) comprising the Anthemideae and the outgroup. Entire leaves then represent a reversal in this character. Entire and variously characteristic leaves have been scored as independent characters, particularly 22–26. The mode of leaf dissection is highly variable and difficult to apply at the generic level. Various types may be present within individual genera. We have designated only a few different types as characters which are absent in the outgroup, particularly 16–21.

In Ursiniinae a number of genera have leaves with secretory cavities, present in floral structures but not in the leaves of many other Anthemideae. Secretory cavities are absent in the outgroup.

Inflorescence

The capitula (inflorescences) are usually terminal either singly at the end of a peduncle or aggregated into a variety of corymbose, spike-like or clustered synflorescences. Sometimes the peduncles are structurally reduced so that the capitula are aggregated into central sessile clusters (an aggregated synflorescence) or, on rare occasions, into a single head (a syncephalum). The capitula are solitary or arranged in lax corymbs in the outgroup and commonly in the Anthemideae. They are also frequently arranged in dense corymbs within certain genera (character 29, further modified as 30). Rarely, the capitula are sessile (34) or solitary on nodding peduncles (33). Within the Artemisiinae the corymbose capitulum arrangement is further modified into a long narrow panicle-like or raceme-like synflorescence (31) generally with numerous capitula. The paniculate-like capitulum arrangement is variable and apparently contains a number of different types. The interpretation of these requires a detailed study, and we have only listed one distinct type as a character, the arrangement of the capitula in glomerules on long spikes (32).

Floral and sex arrangement

The array of sex expressions and floral morphology in most Anthemideae were surveyed by Heywood & Humphries (1977). Radiate, heterogamous capitula with hermaphroditic, perfect disc florets and female ray florets are the plesiomorphic condition, being present in the outgroup. Sometimes the ray florets are neutral but we found this condition difficult to apply as a character at the generic level.

The reduction of the ray florets resulting in discoid, homogamous capitula is common, and has occurred several times within genera. This character (35) has often been used for delimitation of genera, despite its homoplasious nature.

Disciform, heterogamous capitula (36) with central, hermaphroditic florets and outer, female, non-radiate florets occur in several Anthemideae. It is possible to hypothesize two interpretations for discoid and disciform florets. Outer tubular female florets may either be modified central hermaphroditic florets or modified female ray florets. The first hypothesis implies that disciform capitula are derived modifications of discoid capitula. The second hypothesis implies that disciform and discoid capitula may be independently derived from radiate capitula but it is possible also that discoid capitula are derived from disciform capitula by reduction of the outer female florets. For analysis it seemed best to consider discoid and disciform capitula as independent non-additive characters. After construction of the cladogram, a particular interpretation may be considered the most parsi-

monious, as in the case of the Artemisiinae where discoid capitula are considered derived from disciform capitula. In other subtribes discoid capitula are best interpreted as derived directly from radiate capitula. It was eventually seen that there was no support for the hypothesis that disciform capitula are derived from discoid capitula in any group of Anthemideae.

Within Artemisiinae the central florets may have reduced fertility. In *Neopallasia* the central florets are heteromorphic. The florets towards the periphery are perfect and the central ones completely sterile with reduced ovaries (91). In the *Dracunculus* group of the genus *Artemisia*, central floret ovaries are reduced and the florets are functionally male (106).

Involucre

Involucral shape is variable from widely campanulate to narrowly urceolate. In the outgroup the narrow types are absent, so that narrowly urceolate involucres are derived characters (37) within the Anthemideae. The involucral bracts are arranged in several imbricate series as in the outgroup and many other Asteraceae. Rarely there are 4–7 rows (38), more than in the outgroup, or 1–2 rows (39). In one genus (*Eriocephalus*) the involucral bracts are arranged in two distinctly unequal rows without intermediates (40).

In almost all Anthemideae as well as in the outgroup the involucral bracts have scarious margins, otherwise they are generally absent in the Heliantheae. The chaffy bract is one of the main characters (43) which we used to identify the outgroup of the Anthemideae. Sometimes the involucral bracts are wide and flabelliform (41), or have dark brown margins (44), or they are subulate (42), all characters absent in the outgroup.

Receptacle

The receptacle is either paleate or epaleate. Within the Anthemideae the paleate receptacle is plesiomorphic. Formerly the tribe Helenieae was distinguished from Heliantheae by having epaleate receptacles rather than being paleate as in the Heliantheae s.s. Furthermore, the Anthemideae was divided into two subtribes based on receptacular paleae, the paleate Anthemidinae s.l. and the epaleate Chrysantheminae s.l. The homoplasious nature of this character has since long been recognized and the distinction of the Helenieae and the two subtribes of Anthemideae has now been abandoned (see Bremer, 1987).

It seems possible that the epaleate receptacle is a character for a portion of the Heliantheae (s.l.) and Anthemideae. The outgroup of the Anthemideae has epaleate receptacles. Within Anthemideae the presence of a paleate receptacle is hence considered a character (45) despite the fact that it might be under single gene control within certain genera (see Mitsuoka & Ehrendorfer, 1972).

The shape of the receptacle varies from being flat to convex to conical and ultimately subulate. The latter conditions are absent from the outgroup. Receptacle shape is a potential source of more character information but we have found it difficult to interpret at this stage. It is used as a character (46) for a few genera. Rarely the receptacle is hollow (47), pilose (48) or densely hirsute (49), characters absent in the outgroup. The hairs are scattered over the receptacle and similar to hairs on other parts, so that they cannot be hypothesized as being modified paleae. Occasionally, the paleae are also pilose (50) and thus the two characters cannot be considered as homologous (failure of the conjunction test, Patterson, 1982; Humphries & Funk, 1984).

Resin canals

In many genera of the Anthemideae floral parts are frequently invested with resin canals (character 51). They occur in a variety of forms, in the corolla lobes, in style-branches, in cypselas, sometimes in anther tips and often also in the receptacular paleae and involucral bracts. We admit that this generalized character is rather vaguely formulated but offer it as one hypothesis for suggesting the interrelationships of the various subtribes (see discussion below). Resin canals are absent in the outgroup.

Ray florets

The ray corolla limb is yellow in the outgroup and mostly white (character 52) but sometimes yellow in Anthemideae. Glossy golden yellow limbs (53) occur in Leucantheminae and bluish violet limbs (54) in one genus of the Cancriniinae (*Allardia*), although other colours do occur including pink, orange, and red. Occasionally, the limb is deeply emarginate (55). Baagøe (1977) distinguished a number of epidermal cell types on the ray floret limbs. Within the Anthemideae she recognized two groups, with Helianthoid and Senecionoid/Mutisioid epidermal cells (56). The former type occurs in the outgroup. The ray floret tube furnishes a number of rather rare characters not present in the outgroup. The tube is sometimes dorsiventrally flattened (58), laterally pilose (also abaxially on the limb; 59), confluent with the cypsela (60), and persistent on the cypsela (61). Occasionally the ray floret tube sinus extends to the base (57), so that logically the tube is absent.

Outer florets in disciform capitula

Outer female florets and disciform capitula are not present in the outgroup. The characters of the outer female florets listed here mostly represent unique specializations within Artemisiinae where the plesiomorphic and disciform genus *Ajania* serves as an outgroup. Within the Artemisiinae the outer female florets are occasionally subtended by scaphoid bracts (character 64), often their corollas are 'flask-shaped' and tapering above to narrowly cylindrical (65), and rarely the corollas are without teeth (66) or are totally absent (67).

In disciform Anthemideae the outer female florets are sessile and arranged in one row. Rarely in the Matricariinae (*Cotula* group of genera) they are stalked and arranged in several rows (*Soliva*), both very peculiar conditions within the family as a whole. The pluriseriate arrangement is common in other tribes, but is most parsimoniously interpreted as an independent character within the Anthemideae.

Disc florets

The corolla of the disc florets provides several characters. In the outgroup and in many Anthemideae the plesiomorphic condition is seen: yellow, glabrous and actinomorphic, with a more or less distinct, unswollen and non-saccate tube, and a 5-lobed limb without veins or resin sacs in the lobes.

Within the Ursiniinae the corolla is often gradually

expanded and funnel-shaped without distinct tubes and limbs (character 69). In *Sclerorhachis* the limb is contracted at the apex (71). In some genera the corolla is 4-lobed (72). The lobes may be provided with dorsal appendages (73), continuous veins along the margins (74), with central resin sacs (75) or rarely (*Adenoglossa*) with marginal resin canals in two of the lobes which are smaller than the other three (76). Rarely the corolla is red (77) or provided with various types of hairs (78–81, 88, 89).

The corolla tube is sometimes thickened in fruit (82), and in one extreme case (*Oncosiphon*) very thick and brittle (83). It is sometimes saccate basally, adaxially (84) or both abaxially and adaxially (85). In an extreme case (*Otanthus*) the tube is copiously swollen at the base and spongy, and almost enclosing the cypsela (86). Rarely, the tube may be confluent with the cypsela (87, cf. character 60). Other unusual corolla types are those with long-stalked glands as found in the Ursiniinae (89), and those with very thick vascular strands (90).

Anthers

In the outgroup and in most Anthemideae the anthers are not caudate at the base. This was formerly considered an important character for defining the tribe but anther tails (character 92) are present in a few genera. The apical anther appendages are obtuse to rounded in the outgroup and in most Anthemideae. In the Artemisiinae they are triangular-linear-lanceolate and composed of rather thick-walled cells (93). Sometimes the appendages have an apical resin sac (94). The endothecial tissue in the outgroup and many Anthemideae and other Asteraceae is 'non-polarized', i.e. with the endothecial cell wall thickenings arranged evenly. However, in some Anthemideae (and other Asteraceae) the endothecial tissue is 'polarized' (character 95), with the thickenings arranged apically and basally on the cell (Dormer, 1962).

Pollen

Spiny pollen is the plesiomorphic condition of the Anthemideae occurring also in the outgroup. Within the Artemisiinae there is a gradual reduction of the spines (characters 96 and 97) until a rugose appearance is observed on the exine surface. Such a condition is considered a modification associated with wind-pollination (Wodehouse, 1938). In *Adenanthellum*, the pollen is hexa-panto-colporate (98) rather than tricolporate as found generally within the Asteraceae.

Styles

The disc floret style-branches are of the common so-called Senecionoid type: apically penicillate, truncate with parallel stigmatic surfaces. In *Prolongoa* the apical hairs are rather long (character 103), and *Phaeostigma* is named after its brownish style-branches (102). In *Mausolea* (Artemisiinae) the style-branches are not linear as in other disciform Anthemideae but lanceolate, flat and acute (68). Sometimes the style-branches are fused (104) and the style is undivided, a condition associated with functionally male florets.

The style is somewhat bulbous and often situated on a more or less developed stylopodium, as in the outgroup and many Asteraceae. Within Artemisiinae the style base may be slender and parallel-sided (99). Occasionally the stylopodium is large and persistent in fruit (105) and in *Heliocauta* it is modified into a lobed nectary (100). In *Soliva* the style is persistent and spinescent in the mature fruit (101).

Cypselas

The mature and developing cypselas provide a fruitful supply of characters within the Anthemideae (Bruhl & Quinn, 1990; Giroux, 1933; Humphries, 1976, 1977; Khandzhyan, 1983; Kneisl, 1981; Kynclová, 1970; Wilcox, 1977). In the outgroup the cypselas are sharply angled and provided with a heavily carbonized layer. This layer is never present in the Anthemideae but it is widespread throughout the Heliantheae. The reduction of the carbonized layer can be interpreted as a synapomorphy (character 151) for the Anthemideae as a whole. The cypselas of Anthemideae can also be terete to weakly angled, or flattened (107) and modified in various ways. The characters 108–113 relate to different cypsela shapes unique to the ingroup. The cypselas are sometimes much flattened, dorsiventrally (characters 114 and 115) or laterally (116), and the flattened cypselas are often winged (117–122).

Cypselas without a pappus are apically rounded or truncate as in the outgroup, or sometimes provided with an apical rim. It is difficult to say whether this rim is homologous with a short coroniform pappus or is an independent outgrowth of the cypsela wall. We have avoided coding it as a character. In *Oncosiphon* the cypsela rim is distinctly abaxial (123) and seems to be a unique structure.

The presence, number and arrangement of cypsela ribs is very variable. Cypselas with five or four evenly arranged ribs are common and may be plesiomorphic within the tribe. The cypsela ribs are difficult to interpret since similar ribs are absent from the outgroup. Characters 124–129 represent specialized rib structures within Anthemideae. The cypsela ribs are sometimes furnished with resin canals or sacs (131–133, 136, 137), not present in the outgroup. Rarely resin sacs are scattered over the cypsela (138). Within the Leucantheminae, the *Leucanthemum* group is characterized by a unique cypsela type with vallecular resin canals (134) of a particular flattened type and vallecular vascular strands (135), situated in the valleys between the ribs, not inside the ribs (costal) as in other Anthemideae (Briquet, 1916; Briquet & Cavillier, 1916; Giroux, 1933).

Frequently the cypselas are furnished with myxogenic cells within the Anthemideae but the character never occurs in the outgroup. However, it is difficult to apply the presence of myxogenic cells as a simple presence or absence character as it is homoplasious within the tribe as a whole. The myxogenic cells are commonly situated along the ribs and this appears to be the plesiomorphic arrangement. Other particular distributions of the myxogenic cells may serve as characters (139–141, 143). Characters 142 and 144 represent unique myxogenic cell shapes, quite different from the common type which consists of transversely compressed cells in elongated rows.

The cypselas of the Anthemideae are generally smooth and glabrous or sometimes covered with scattered glands. Glabrous and sparsely to rather densely hirsute cypselas are found in the outgroup. Papillose cypselas (145) and cypselas with other types of indumentum not present in the outgroup are those represented by characters 146–150.

The cypsela wall is sometimes several cell layers thick and partially or completely sclerified (152). In other cases it is very thin (characters 154 and 155). The intermediate condition is common and present in the outgroup. The anatomy of

the cypsela wall is a potential source of more character information but detailed investigations of the appropriate genera are necessary. The investigations by Reitbrecht (1974) need to be expanded and performed in more detail (see Bruhl & Quinn, 1990 on the 'Cotuleae'). Characters 156, 159 and 160 represent unique specializations within the Anthemideae (Källersjö, 1986, 1988). The cells of the cypsela wall usually contain isodiametric druses as in many Asteraceae. Rarely they are numerous (158) and in *Prolongoa* they are replaced by rod-shaped crystals in small packets (157).

Pappus

In the Anthemideae the cypselas are generally without a pappus or provided with a coroniform or scaly pappus. True bristles, which are never flattened and occur in other tribes, are never present. Such bristles are absent also from the outgroup, where the pappus, if present, consists of large whitish scales or numerous whitish, long, flat bristles (more properly bristle-like linear scales). Similar pappus types are present in Ursiniinae (*Ursinia*) and Cancriniinae and we assume that the presence of large or long-whitish pappus scales are plesiomorphic within the tribe. The five convolute-contorted pappus scales (character 164) of *Ursinia* seem to be unique for that genus, although the large size and the whitish colour appear to be plesiomorphic. A reduced or lost pappus is represented by characters 161, 171 and 172 within the Anthemideae. The coroniform pappus is either derived from fusion of the individual pappus scales or is an independent character unique to the Anthemideae. If we adopt the latter hypothesis, logically the coroniform pappus seems to be a plesiomorphic condition within the Anthemideae, excluding Ursiniinae and Cancriniinae, whereas specialized corona types and auricles are apomorphic, particularly as seen with characters 162, 163 and 165–170.

Testa

Testa epidermal types were investigated by Kneisl (1981), but the results are difficult to interpret. The testa epidermis cells are normally well developed with sinuose cells. Sometimes the testa collapses during maturation of the fruit. Rarely the testa epidermis cells are uniquely specialized, much elongated and spirally arranged around the embryo (character 173) or thick-walled and dark reddish (174).

Embryology

The Anthemideae have been fairly thoroughly investigated compared to many other tribes, by Harling (1950, 1951, 1960). Tetrasporic embryo sacs (character 175) unambiguously characterize a number of genera, and disporic embryo sacs (176) are reported as unique within *Argyranthemum* (Borgen, 1972). Harling also described development of the embryo sacs in detail but the variation is difficult to formulate into characters.

Chromosome numbers

The Anthemideae have been investigated based on the surveys of Federov (1969), Moore (1972, 1973, 1977), and Goldblatt (1980, 1981, 1984). X=9 is the base number for the tribe. Most genera have either a diploid number of 2n=18 or 2n=36. *Cancrinia* has a base number of x=7, *Ursinia* a base number of x=7, 8, and *Artemisia* a series based on x=5, 6, 7, 8 and 9. The highest values have been recorded in *Leptinella* with 2n=312 (Lloyd, 1972a). Most series and most variants are aneuploid or polyploid series within genera and variation is of little use for classification at the generic level. However, it appears that the base number of x=10 (character 177) as opposed to x=9 is plesiomorphic to a number of genera in the Thaminophyllinae and Matricariinae (*Cotula* group).

Chemistry

Chemical characters are difficult to utilize because they are mostly collected on a sporadic basis for one or two species within a genus. Furthermore, it is rare to find phytochemical papers that report absence traits as well as presence of a chemical. However, the Anthemideae are well-known for accumulating herbal and insecticidal chemicals and relative to many angiosperms have been richly studied (Greger, 1975, 1977; Bohlmann et al., 1973). For systematic purposes available chemical evidence suggests that sesquiterpene lactones (character 179), flavonoids (182), particularly C-glycosyl flavones (Valant-Vetschera, 1981, 1982, 1985) and polyacetylenes (183) are of most systematic value (Greger, 1977; Tétényi, 1986).

Presence of a chemical character has been scored at generic rank even though it is acknowledged that investigation has been sporadic, particularly with the larger genera, such as *Artemisia*. The scores thus represent hypothetical presence for all the species. Different compounds within the same class of compounds have been combined into a single score for polyacetylenes (183) and furanosesquiterpenes (179) when the class compound is considered apomorphic for a particular group. Red coloured root tips, due to the presence of anthocyanin (184) has been recorded in *Leucanthemum* (Favarger, 1966).

DISTRIBUTION

The approximate total range of the Anthemideae is summarized in Table 3 and the general distribution of subtribes and genera given in Tables 3, 5, 7, 9, 11, 14, 16, 18, 20, 22 and 24; see taxonomic text below. The Anthemideae tribe has a worldwide distribution but with main concentrations of taxa in Central Asia, the Mediterranean region and South Africa. Some members of the subtribes Ursiniinae, Artemisiinae, Chrysantheminae, Leucantheminae, Anthemidinae, and Matricariinae are pernicious weeds, such as some of the *Ursinia* species introduced to Australia and New Zealand, and species of *Chrysanthemum*, *Anthemis*, *Artemisia*, *Achillea*, *Leucanthemum*, *Tripleurospermum* and *Matricaria* as more widespread weeds in both the northern and southern hemispheres. However, most taxa have discrete ranges and very obvious areas of endemism. The Thaminophyllinae, for example, occur only in South Africa. Similarly most Ursiniinae are almost entirely restricted to South Africa, although one species of *Ursinia* occurs in Ethiopia and another species of *Lasiospermum* is found in the Sinai region of Egypt.

The Gonosperminae is a small subtribe of three genera and 15 species which displays a presumably relictual distribution pattern. *Gonospermum* and *Lugoa* are endemic to the Canary Islands but have a curious disjunct distribution pattern with their sister genus, *Inulanthera*, which has ten species

Table 3 Summary of geography and natural distribution of the Anthemideae.

	N.Am.	Eur-Asia	C.& E. Asia	SW Asia	S.Eur	N.Afr	S.Afr	Austr. N.Zeal.	S.Am.
Number of genera	8	25	38	13	28	38	29	3	4
Ursiniinae						2	8		
Cancriniinae			6	1					
Tanacetinae	1	2	6	2	1	1			
Gonosperminae						2	1		
Handeliinae		5	4						
Artemisiinae	4	4	15	4	2	1	1		1
Achilleinae		5	2	2	5	7			
Anthemidinae		1		1	1	1			
Chrysantheminae		1		1	2	4			
Leucantheminae		3	2		12	11			
Thaminophyllinae							5		
Matricariinae	3	4	3	2	5	10	14	3	3

in southern Africa, mainly in Natal, but with one species also occurring in Madagascar.

The majority of the remainder of the tribe occur in the northern hemisphere. For example, the Chrysantheminae are most prominent in North Africa and Macaronesia, although the two well-known species of *Chrysanthemum*, *C. coronarium* and *C. segetum* are widespread throughout the northern hemisphere. Indeed, *C. coronarium* is cultivated widely as a salad vegetable in China. By contrast, the Leucantheminae are found in Eurasia and North Africa, and are particularly concentrated in the Mediterranean region. The Achilleinae is more of a Eurasian group with some of the more distinctive taxa endemic to North Africa, southern Europe, the Mediterranean, and South-West Asia, although there are some outlying taxa occuring in North America. The 'Tanacetinae' are well-represented in Eurasia and especially in central Asia but there are some interesting endemics which occur also in North America and North Africa. The Cancriniinae and Handeliinae are comprised of eleven genera and thirty-four species restricted entirely to the central steppes of Asia. The Artemisiinae and Matricariinae are the most widespread subtribes. The Artemisiinae which comprise about a third of the tribe, with 18 genera and more than six hundred species currently recognized, have a worldwide distribution but occur mainly in the northern hemisphere and especially central and eastern Asia. The Matricariinae, comprised of 25 genera and about 250 species, also has a worldwide distribution but most genera occur in the Mediterranean region and South Africa.

KEY TO GENERA

1 Receptacle distinctly paleate with paleae subtending florets (in *Anthemis* rarely with the basal part of the conical receptacle epaleate) 2
Receptacle completely epaleate (though sometimes pilose or hirsute) or capitula few-flowered and presence of paleae unclear 41

2 Capitula radiate; rays present 3
Capitula discoid or disciform; rays absent 22

3 Rays yellow, rarely abaxially reddish 4
Rays white or rarely pink to reddish on both sides 11

4 Capitula sessile ..... 56. **Cladanthus**
Capitula pedunculate 5

5 Pappus of 5 (rarely 8–10) large obovate scales and sometimes 5 additional subulate scales (pappus rarely absent in *Ursinia trifida*, a South African shrub with linear, entire or apically few-lobed leaves) ..... 1. **Ursinia**
Pappus a shallow corona, an auricle or rarely of few small scales, or absent 6

6 Disc cypselas 5-ribbed, without pappus; ray cypselas flat and sterile with a few pappus scales; leaves serrate ..... 63. **Lepidophorum**
Cypselas equal, without or with a coroniform or auriculiform pappus; leaves various 7

7 Cypselas obovoid without distinct ribs or wings 8
Cypselas angled or ribbed or prismatic, often turbinate, sometimes tuberculate; or cypselas flattened and with 2 lateral ribs or wings 9

8 Leaves few-lobed or entire ..... 53. **Mecomischus**
Leaves pinnatifid to pinnatisect ..... 54. **Chamaemelum**

9 Cypselas dorsiventrally flattened and with 2 lateral ribs or broad wings 10
Cypselas various, sometimes dorsiventrally flattened but then rhombic in cross-section and not or only narrowly winged ..... 57. **Anthemis**

10 Cypselas with 2 lateral more or less distinct ribs but no wings ..... 50. **Achillea**
Cypselas with 2 lateral wings ..... 51. **Anacyclus**

11 Pappus of 5 (rarely 8–10) large obovate scales and sometimes 5 additional subulate scales. ..... 1. **Ursinia**
Pappus a shallow corona, an auricle, or of small scales, or absent 12

12 Cypselas copiously villous ..... 2. **Lasiospermum**
Cypselas glabrous, sometimes glandular or papillose 13

13 Involucral bracts in 2 unequal series; one outer row of pubescent to glabrescent bracts and one inner row of generally densely villous bracts ..... 108. **Eriocephalus**
Involucral bracts imbricate and subequal, not in 2 unequal series 14

14 Shrubs with opposite leaves (leaves alternate in *Eumorphia davyi*, a South African shrub with linear, closely set leaves); cypselas with 10 or more ribs ..... 4. **Eumorphia**
Herbs or rarely shrubs with alternate leaves (rarely with some leaves opposite basally on the stems); cypselas various 15

15 Suffruticose perennial with large leaves with rounded lobes and

corymbose capitula; cypselas 5-ribbed with pappus of small scales projected from the ribs ..... 22. **Lugoa**
Habit and cypselas various but leaves not large and with rounded lobes and pappus if present not of scales projected mainly from the ribs 16

16 Cypselas obovoid, without distinct ribs or wings 17
Cypselas angled or ribbed or prismatic, often turbinate, sometimes tuberculate; or cypselas flattened and with 2 lateral ribs or wings 18

17 Leaves few-lobed or entire ..... 53. **Mecomischus**
Leaves pinnatifid to pinnatisect ..... 54. **Chamaemelum**

18 Cypselas dorsiventrally flattened and with 2 lateral ribs or broad wings 19
Cypselas various, sometimes dorsiventrally flattened but then rhombic in cross-section and without 2 lateral ribs and not or only narrowly winged 21

19 Cypselas with 2 lateral more or less distinct ribs but no wings ..... 50. **Achillea**
Cypselas with 2 lateral wings 20

20 Leaves vermiform; disc corolla tube deeply and equally saccate both adaxially and abaxially ..... 52. **Leucocyclus**
Leaves pinnatisect; disc corolla tube adaxially slightly saccate ..... 51. **Anacyclus**

21 Leaves serrate-dentate, rarely pinnatifid or entire; anthers caudate ..... 79. **Osmitopsis**
Leaves pinnatisect to variously lobed; anthers not caudate 57.**Anthemis**

22 Pappus present, of scales, an auricle or a corona 23
Pappus absent, but cypselas sometimes apically with an obtuse rim (rarely with a pseudopappus of bristle-like stalked glands in *Athanasia*) 28

23 Pappus of 5 (rarely 8–10) large obovate scales and sometimes 5 additional subulate scales ..... 1. **Ursinia**
Pappus a shallow corona, an auricle or of small scales 24

24 Capitula solitary or laxly corymbose ..... 57. **Anthemis**
Capitula densely corymbose 25

25 Glabrous annual herb; cypselas with 1 adaxial and 2 lateral ribs and with a single secretory cavity apically in the adaxial rib ..... 97. **Lonas**
More or less pubescent shrubs; cypselas 5–10-ribbed with or without several secretory cavities in the ribs 26

26 Capitula narrowly oblong-obconical, slender, and few-flowered; indumentum of stellate hairs ..... 6. **Hymenolepis**
Capitula rather widely urceolate to cyathiform-campanulate; indumentum of simple or bifid hairs 27

27 Cypselas 5-ribbed; anthers not caudate ..... 23. **Gonospermum**
Cypselas 8–10-ribbed; anthers caudate ..... 24. **Inulanthera**

28 Cypselas copiously villous ..... 2. **Lasiospermum**
Cypselas glabrous, sometimes glandular 29

29 Involucral bracts in 2 unequal series; one outer row of pubescent to glabrescent bracts and one inner row of generally densely villous bracts ..... 108. **Eriocephalus**
Involucral bracts imbricate and subequal, not in 2 unequal series 30

30 Leaves entire or crenate, covered with a dense greyish-white indumentum; corolla tube basally copiously swollen and spongy, almost enclosing the cypsela especially laterally ..... 49. **Otanthus**
Leaves various; corolla tube not or somewhat swollen and spongy but not enclosing the cypsela 31

31 Cypselas obovoid without distinct ribs or wings 32
Cypselas angled or ribbed or prismatic, often turbinate, sometimes tuberculate; or cypselas flattened and with 2 lateral ribs or wings 34

32 Capitula numerous in a long panicle ..... 41. **Seriphidium**
Capitula solitary or laxly corymbose or few closely together 33

33 Capitula almost sessile along the stems ..... 55. **Rhetinolepis**
Capitula pedunculate ..... 54. **Chamaemelum**

34 Cypselas dorsiventrally flattened and with 2 lateral ribs or broad wings 35
Cypselas various, sometimes dorsiventrally flattened but then rhombic in cross-section and not or only narrowly winged . 37

35 Cypselas with 2 lateral more or less distinct ribs but no wings 36
Cypselas with 2 lateral wings ..... 51. **Anacyclus**

36 Leaves mainly rosulate and capitula solitary; cypselas actually 4–5-ribbed though with 2 major lateral ribs ..... 21. **Heliocauta**
Leaves alternate and capitula often corymbose, rarely solitary; cypselas with 2 lateral ribs only ..... 50. **Achillea**

37 Shrublets; corolla basally saccate around the cypsela especially adaxially ..... 48. **Santolina**
Herbs or shrubs; corolla not saccate basally 38

38 Shrubs with stellate hairs if present; corolla gradually expanded and funnel-shaped ..... 7. **Athanasia**
Herbs or half-shrubs with simple or bifid hairs; corolla more or less distinctly divided into tube and limb 39

39 Basally villous perennials with much pinnatisect, mainly basal leaves; cypselas 4–5-ribbed 40
Indumentum various but not mainly basal and villous; annuals or perennials; leaves and cypselas various ..... 57. **Anthemis**

40 Stems few-branched, leafy and with terminal corymbs ..... 28. **Handelia**
Stems loosely branched, almost leaf-less with terminal capitula ..... 29. **Sclerorhachis**

41 Capitula radiate; rays present 42
Capitula discoid or disciform; rays absent 109

42 Rays yellow, rarely partly white or reddish or abaxially reddish 43
Rays white, rarely pink to reddish, bluish violet or creamy orange, but not yellow 62

43 Pappus present in ray or disc cypselas or generally in all cypselas, of scales, an auricle or a corona (sometimes almost absent in *Tanacetum* but cypselas then apically with an acute rim) 44
Pappus absent but cypselas sometimes apically with an obtuse rim (in *Argyranthemum* sometimes with pappus-like apically projected cypsela wings) 54

44 Cypselas densely pilose; pappus of 4–12 white scales at least half as long as the corolla ..... 9. **Trichanthemis**
Cypselas glabrous, sometimes glandular; pappus of short scales, a corona or an auricle 45

45 Cypselas dorsiventrally flattened and with 2 lateral broad wings; an annual herb with entire, fleshy leaves ..... 101. **Adenoglossa**
Cypselas various, sometimes dorsiventrally flattened but then not or only narrowly winged and often rhombic in cross-section 46

46 Disc corolla 4-lobed; leaves entire ..... 81. **Inezia**
Disc corolla 5-lobed; leaves various 47

47 Cypselas with 1 adaxial and 2 lateral distinct ribs, abaxially with

or without 2 weaker ribs; pappus coroniform if present 48
Cypselas various, generally with 5 or more ribs and not with 3 major adaxial-lateral ribs; pappus and habit various 49

48 Leaves pinnatifid-pectinate; cypselas with 3 adaxial-lateral thick ribs and 2 abaxial weaker ribs; pappus absent in disc cypselas but present in ray cypselas ..... 70. **Prolongoa**
Leaves pinnatisect; cypselas with 3 adaxial-lateral acute ribs; pappus present in both disc and ray cypselas . 94. **Endopappus**

49 Cypselas 8–12-ribbed with dark vallecular secretory canals between the pale ribs; annuals 50
Cypselas angled, prismatic or ribbed, but vallecular secretory canals absent; annuals or perennials 53

50 Pappus a scarious, adaxial, flabelliform auricle, as long as the corolla or longer ..... 76. **Glossopappus**
Pappus a corona, a short auricle, or absent 51

51 Leaves lobed, often trifurcate; disc cypselas with a stiff coroniform pappus ..... 75. **Chrysanthoglossum**
Leaves serrate-dentate; disc cypselas without or with a scarious, coroniform or auriculiform pappus 52

52 Rays golden yellow; cypselas arcuate with the ribs basally and adaxially fused into a more or less distinct callus ..... 77. **Coleostephus**
Rays pale yellow; cypselas ellipsoid without a basal callus ..... 73. **Leucoglossum**

53 Cypselas with myxogenic cells on the ribs; pappus a scarious flimsy corona; creeping or caespitose suffruticose perennials ..... 68. **Leucanthemopsis**
Cypselas without myxogenic cells; habit and pappus various ..... 15. **Tanacetum**

54 Ray cypselas triquetrous, winged; disc cypselas laterally flattened and adaxially and abaxially winged or sometimes terete to prismatic 55
Cypselas equal, oblong or obovoid, without wings, or dorsiventrally flattened and laterally winged 58

55 Shrubs or shrublets ..... 62. **Argyranthemum**
Annual herbs 56

56 Plant covered with viscid hairs; cypsela wings projected to apical spines ..... 60. **Heteranthemis**
Plants not viscid; cypsela wings if present not projected to apical spines 57

57 Disc corolla red; disc cypselas laterally flattened and adaxially and abaxially winged ..... 61. **Ismelia**
Disc corolla yellow; disc cypselas prismatic with a narrow adaxial wing or terete and apparently ribbed ..... 59. **Chrysanthemum**

58 Disc corolla 4-lobed; rays not true ray florets but outer disc florets with one corolla lobe expanded to a limb; cypselas dorsiventrally flattened ..... 103. **Cotula**
Disc corolla 5-lobed; rays true ray florets with apically 3-lobed limbs; cypselas oblong or obovoid 59

59 Cypselas distinctly ribbed with dark vallecular secretory canals between the pale ribs ..... 71. **Leucanthemum**
Cypselas distinctly or faintly ribbed but vallecular secretory canals absent 60

60 Basally much woody shrublets with few-lobed leaves with linear lobes ..... 30. **Brachanthemum**
Herbs or half-shrubs; leaves generally with rather broad lobes 61

61 An annual herb with few-lobed leaves ..... 33. **Tridactylina**
Perennials; leaves various ..... 31. **Dendranthema**

62 Pappus present at least in ray cypselas, of scales (bristle-like in *Allardia*), an auricle or a corona (sometimes almost absent in *Tanacetum* but cypselas then apically with an acute rim) ... 63
Pappus absent but cypselas sometimes apically with an obtuse rim (mainly abaxial and somewhat toothed in *Oncosiphon*; cypselas in *Argyranthemum* sometimes with pappus-like apically projected wings) 88

63 Pappus of 4–12 linear to obovate-oblong scales at least half as long as the corolla, or of many bristle-like scales as long as the corolla or longer 64
Pappus of short scales, an auricle or a corona 66

64 Pappus of 4–12 scales half to equalling the corolla in length; rays white or sometimes pink 65
Pappus of many bristle-like scales equalling or exceeding the corolla in length; rays often bluish-violet, sometimes white or pink ..... 12. **Allardia**

65 Cypselas densely pilose; pappus scales white ..... 9. **Trichanthemis**
Cypselas glabrous, glandular; pappus scales brownish ..... 11. **Richteria**

66 Cypselas 8–12-ribbed with dark vallecular secretory canals between the pale ribs 67
Cypselas angled, prismatic or often ribbed, but vallecular secretory canals absent 69

67 Annuals; cypselas *c.* 1 mm long ..... 73. **Leucoglossum**
Perennials; cypselas more than 1 mm long 68

68 Leaves entire or serrate or pinnatifid, sessile; cypsela ribs rounded ..... 71. **Leucanthemum**
Leaves trifid or ternate-pinnatifid and seemingly petiolate; cypsela ribs narrow and somewhat wing-like ..... 72. **Rhodanthemum**

69 Cypselas triquetrous with 1 adaxial and 2 lateral more or less thick ribs and sometimes with 1–2 abaxial weaker ribs, abaxially and apically with 2 distinct (occasionally fused to 1 or 3–5) resin sacs ..... 98. **Tripleurospermum**
Cypselas various, sometimes triquetrous with 3 adaxial-lateral ribs but not with 2 abaxial-apical resin sacs 70

70 Annual herbs 71
More or less suffruticose perennials, shrublets or shrubs ... 81

71 Cypselas laterally pilose; pappus a fimbriate whitish corona (disc cypselas) or auricle (ray cypselas) ..... 93. **Microcephala**
Cypselas glabrous; sometimes glandular; pappus various ... 72

72 Ray cypselas dorsiventrally flattened and laterally winged; disc cypselas 5-ribbed ..... 91. **Daveaua**
Cypselas equal or subequal, sometimes somewhat flattened but not winged, variously ribbed 73

73 Cypselas somewhat dorsiventrally flattened and with 2 lateral weak ribs; corolla lobes with central resin sacs ..... 99. **Aaronsohnia**
Cypselas with 3 or more, sometimes adaxial, more or less distinct ribs, sometimes slightly flattened; corolla lobes without or sometimes with central resin sacs (in *Matricaria*) 74

74 Cypselas with 1 abaxial (not adaxial) and 2 lateral thick ribs and 2–3 adaxial weaker ribs; pappus an adaxial stiff auricle ..... 89. **Otospermum**
Cypselas with mainly adaxial-lateral ribs or with ribs all around the cypsela; pappus of scales, a scarious auricle or a corona . 75

75 Cypsela wall and pappus white and spongy, abaxially thin ..... 96. **Foveolina**
Cypsela wall not white and spongy, pappus scarious 76

76 Cypselas with 1 adaxial and 2 lateral distinct ribs, abaxially with or without 2 weaker ribs, or cypselas with 5 adaxial-lateral

ribs 77
Cypsela ribs all around the cypsela, not mainly adaxial-lateral 79

77 Cypselas with 1 adaxial and 2 lateral distinct ribs, abaxially with or without 2 weaker ribs; pappus of scales or a stiff corona . 78
Cypselas with 5 adaxial-lateral ribs; pappus an auricle or a small corona ..... 92. **Matricaria**

78 Cypselas with 3 adaxial-lateral rounded ribs and 2 abaxial weaker ribs, often with 3–5 resin sacs apically in the ribs; pappus of 7–10 obovate scales ..... 90. **Heteromera**
Cypselas with 3 adaxial-lateral acute ribs; pappus a stiff corona ..... 94. **Endopappus**

79 Pappus a scarious, flimsy corona; cypselas with myxogenic cells on the ribs; leaves pinnatifid-pectinate, spathulate in outline ..... 69. **Hymenostemma**
Pappus coroniform, of short more or less connate scales, or an auricle; cypselas with or without myxogenic cells; leaves various 80

80 Cypselas obconical-turbinate, generally with myxogenic cells; slender annuals with several stems from a basal rosette (*Anthemis* subgen. *Ammanthus*) ..... 57. **Anthemis**
Cypselas more or less oblong, without myxogenic cells; habit various ..... 15. **Tanacetum**

81 More or less suffruticose perennials 82
Woody shrubs or shrublets 84

82 Cypselas with myxogenic cells on the ribs 83
Cypselas without myxogenic cells ..... 15. **Tanacetum**

83 Pappus a scarious, flimsy corona; leaves serrate to pinnatifid, generally pectinate and spatulate in outline ..... 68. **Leucanthemopsis**
Pappus of separate, mainly abaxial scales; leaves pinnatisect ..... 16. **Opisthopappus**

84 Cypselas dorsiventrally flattened and laterally winged ..... 100. **Leucoptera**
Cypselas more or less terete, not winged 85

85 Leaves obovate and apically serrate ..... 64. **Nipponanthemum**
Leaves pinnatisect to variously lobed 86

86 Pappus an adaxially longer cup, or one large adaxial and one smaller abaxial scale; cypselas with myxogenic cells ..... 84. **Cymbopappus**
Pappus a small corona, of several scales or an adaxial auricle; cypselas with or without myxogenic cells 87

87 Cypselas with myxogenic cells; pappus of several adaxially longer scales ..... 18. **Xylanthemum**
Cypselas without myxogenic cells; pappus a corona of small scales or an adaxial auricle ..... 15. **Tanacetum**

88 Ray cypselas triquetrous, winged; disc cypselas laterally flattened and adaxially and abaxially winged 89
Cypselas generally equal, sometimes triquetrous or dorsiventrally (not laterally) flattened and laterally (not adaxially and abaxially) winged 90

89 Annual herb ..... 61. **Ismelia**
Shrubs or shrublets ..... 62. **Argyranthemum**

90 Disc corolla 4-lobed 91
Disc corolla 5-lobed 97

91 Leaves entire, lanceolate to linear ..... 83. **Thaminophyllum**
Leaves variously lobed or pinnatisect, not entire 92

92 Disc corolla tube very much swollen and brittle ..... 88. **Oncosiphon**
Disc corolla tube not or only slightly swollen 93

93 Delicate, somewhat succulent, annual herb; leaves with rounded lobes; capitula small, 5 mm or less in diam. ..... 58. **Nananthea**
Annuals or perennials; leaves various; capitula generally more than 5 mm in diam. 94

94 Leaves with few, oblong to rounded, apically mucronate lobes; receptacle pilose ..... 82. **Lidbeckia**
Leaves variously pinnatisect; receptacle glabrous 95

95 Cypselas with 5 adaxial-lateral ribs, somewhat flattened; annuals ..... 92. **Matricaria**
Cypselas flattened and with 2 lateral ribs, or obovoid and with 2–3 faint ribs; perennials or rarely annuals 96

96 Shrub; cypselas subglobose with 2–3 adaxial faint ribs ..... 102. **Hilliardia**
Herbs; cypselas dorsiventrally flattened and with 2 lateral ribs ..... 103. **Cotula**

97 Leaves opposite 98
Leaves alternate 99

98 Shrubs with entire or few-lobed leaves ..... 4. **Eumorphia**
Creeping, suffruticose perennials with serrate-pinnatifid leaves ..... 67. **Phalacrocarpum**

99 Cypselas triquetrous, with 1 adaxial and 2 lateral more or less thick ribs and sometimes with 2 abaxial weaker ribs, abaxially and apically with 2 distinct (occasionally fused to 1 or 3–5) resin sacs ..... 98. **Tripleurospermum**
Cypselas various, generally with 5 or more ribs, or with 2 lateral ribs only 100

100 Cypselas somewhat dorsiventrally flattened, with 5 adaxial ribs or with 2 lateral ribs only 101
Cypselas more or less terete with 5 or more ribs all around the cypsela 102

101 Cypselas smooth, with 2 lateral weak ribs .... 99. **Aaronsohnia**
Cypselas with 5 adaxial-lateral ribs ..... 92. **Matricaria**

102 Cypselas distinctly ribbed with dark vallecular secretory canals between the pale ribs ..... 71. **Leucanthemum**
Cypselas distinctly or faintly ribbed but vallecular secretory canals absent 103

103 Disc corolla tube confluent with the cypsela; cypsela ribs with resin canals; leaves serrate ..... 80. **Adenanthellum**
Disc corolla tube not confluent with the cypsela; cypsela ribs without resin canals; leaves various 104

104 Cypselas 10–18-ribbed with ovoid myxogenic trichomes; shrubs or half-shrubs with entire or few-lobed leaves ..... 3. **Phymaspermum**
Cypselas generally with less than 10 ribs, with or without appressed myxogenic cells but not with ovoid myxogenic trichomes; habit and leaves various 105

105 Annual herb with lobed, rather lacerate leaves; cypselas without myxogenic cells ..... 66. **Nivellea**
Perennials; leaves various; cypselas with or without myxogenic cells 106

106 Basally much woody shrublets with few-lobed leaves with linear lobes ..... 30. **Brachanthemum**
Herbs or half-shrubs generally with rather broad leaf-lobes or with linear or serrate leaves 107

107 Cypselas oblong, more or less distinctly ribbed, without myxogenic cells 108
Cypselas obovoid, faintly ribbed, mostly with myxogenic cells ..... 31. **Dendranthema**

108 Leaves mostly rosulate; ray florets fertile . 32. **Arctanthemum**
Leaves alternate; ray florets sterile ..... 65. **Leucanthemella**

109 Cypselas triquetrous with 1 adaxial and 2 lateral more or less thick ribs and sometimes with 2 abaxial weaker ribs, abaxially and apically with 2 distinct (occasionally fused to 1 or 3–5) resin sacs ..... 98. **Tripleurospermum**
Cypselas various, sometimes triquetrous with 3 adaxial-lateral ribs but not with 2 abaxial-apical resin sacs 110

110 Pappus present, of scales (bristle-like in *Ugamia*), an auricle or a corona (rarely almost absent in *Tanacetum* but cypselas then apically with an acute rim) 111
Pappus absent but cypselas sometimes apically with an obtuse rim (mainly abaxial and somewhat toothed in *Oncosiphon*; rarely with a pseudopappus of bristle-like stalked glands in *Athanasia*) 138

111 Annual herbs 112
Perennial herbs or often half-shrubs, shrublets or shrubs . 120

112 Cypselas conspicuously rugose to tuberculate, without ribs, apically with a thick, spreading to revolute pappus-like rim ..... 87. **Rennera**
Cypselas often ribbed and not rugose to tuberculate, or if rugose then also with 3 distinct adaxial-lateral ribs; pappus of scales, a corona (but not thick and spreading to revolute) or an auricle 113

113 Cypselas somewhat dorsiventrally flattened and with 2 lateral weak ribs; corolla lobes with central resin sacs ..... 99. **Aaronsohnia**
Cypselas with 3 or more, sometimes adaxial, more or less distinct ribs, sometimes slightly flattened; corolla lobes without or sometimes with central resin sacs (in *Matricaria*) 114

114 Cypselas laterally pilose; pappus a fimbriate whitish corona ..... 93. **Microcephala**
Cypselas glabrous, sometimes glandular; pappus various . 115

115 Cypsela wall and pappus white and spongy, abaxially thin ..... 96. **Foveolina**
Cypsela wall not white and spongy; pappus scarious 116

116 Cypselas with 1 adaxial and 2 lateral distinct ribs, abaxially with or without 2 weaker ribs, or cypselas with 5 adaxial-lateral ribs 117
Cypsela ribs all around the cypsela, not mainly adaxial-lateral 118

117 Cypselas with 1 adaxial and 2 lateral more or less thick ribs; pappus a stiff corona covered with myxogenic cells ..... 95. **Myxopappus**
Cypselas with 5 adaxial-lateral ribs; pappus an auricle or a small corona ..... 92. **Matricaria**

118 Cypselas with dark vallecular secretory canals between the pale ribs and with myxogenic cells on the ribs; pappus an adaxial but basally coroniform auricle as long as the corolla or longer ..... 74. **Chlamydophora**
Cypselas without vallecular secretory canals, with or without myxogenic cells; pappus of small scales, a small corona or auricle 119

119 Cypselas obconical-turbinate, generally with myxogenic cells; slender annuals with several stems from a basal rosette (*Anthemis* subgen. *Ammanthus*) ..... 57. **Anthemis**
Cypselas more or less oblong, without myxogenic cells; habit various ..... 15. **Tanacetum**

120 Pappus of 4–15 linear and bristle-like to obovate-oblong scales at least half as long as the corolla 121
Pappus of short scales, an auricle or a corona 123

121 Cypselas densely pilose; pappus scales white 122
Cypselas glabrous or sparsely pilose; pappus scales brownish ..... 13. **Cancrinia**

122 Capitula on short, nodding peduncles ..... 10. **Ugamia**
Capitula on elongated, straight peduncles or pedunculoid stems ..... 9. **Trichanthemis**

123 Cypselas with dark vallecular secretory canals between the pale ribs and with myxogenic cells on the ribs; pappus an adaxial auricle ..... 78. **Plagius**
Cypselas without vallecular secretory canals; pappus of scales, a corona or sometimes an auricle 124

124 Capitula small and numerous in an elongated panicle or a large corymb; basally villous and woody perennials with much pinnatisect leaves 125
Capitula and leaves various, sometimes small and rather many in a panicle or corymb but plant then not basally villous with much pinnatisect leaves; perennial herbs, half-shrubs, shrublets or shrubs 126

125 Capitula in an elongated panicle ..... 25. **Lepidolopsis**
Capitula in a large corymb ..... 26. **Polychrysum**

126 Capitula paniculate; leaves apically few-lobed or entire ..... 42. **Crossostephium**
Capitula solitary or laxly to densely corymbose or closely aggregated; leaves various 127

127 A compact, hirsute, basally woody half-shrub with solitary, pecunculate capitula; cypselas distinctly 10-ribbed with a coroniform pappus of short wide scales ..... 14. **Cancriniella**
Habit and cypselas various, often perennial herbs or shrubs 128

128 Capitula closely aggregated at the stems; leaves small, ericoid, entire or occasionally few-lobed; pappus of 7–10 oblong, adaxially longer scales ..... 86. **Marasmodes**
Capitula solitary or laxly to densely corymbose; leaves and pappus various 129

129 Capitula narrowly oblong-obconical, slender and few-flowered; pubescent shrubs; indumentum of stellate hairs ..... 6. **Hymenolepis**
Capitula generally urceolate to cyathiform or campanulate; habit various; indumentum if present of simple or bifid hairs 130

130 Shrub with corymbose capitula and pinnatisect leaves; cypselas 8–10-ribbed; pappus of small scales projecting from the cypsela ribs ..... 24. **Inulanthera**
Pappus of scales not distinctly projecting from the cypsela ribs, a corona or an auricle; habit and cypselas various 131

131 Pollen smooth; a small densely pubescent, basally woody perennial with solitary or few capitula on short peduncles (*Sphaeromeria compacta*) ..... 39. **Sphaeromeria**
Pollen spiny; habit and capitula various 132

132 Shrublets with entire or 3-lobed leaves; capitula rather narrowly urceolate with involucral bracts in 5–7 rows; pappus of many subulate scales ..... 19. **Lepidolopha**
Habit, capitula and pappus various, if shrubby with entire or 3-lobed leaves (some *Pentzia* species), then not with involucral bracts in 5–7 rows and not with a pappus of subulate scales 133

133 Capitula disciform; outer female florets present; cypselas without myxogenic cells ..... 15. **Tanacetum**
Capitula discoid; all florets hermaphrodite; cypselas with or without myxogenic cells 134

134 Corolla tube generally swollen and with thick vascular strands; shrubs with more or less ericoid leaves ..... 85. **Pentzia**
Corolla tube not or only slightly swollen and with thin vascular strands; habit and leaves various 135

135 Pappus an adaxial auricle or of several adaxially more devel-

oped scales 136
Pappus a corona or of scales, adaxially not more developed 137

136 Perennial herbs with corymbose capitula ..... 15. **Tanacetum**
Shrublets with solitary capitula ..... 18. **Xylanthemum**

137 Leaves entire but marginally crenate-serrate; perennial herb (*Tanacetum balsamita*) ..... 15. **Tanacetum**
Leaves pinnatisect; habit various ..... 17. **Tanacetopsis**

138 Leaves opposite; shrubs with sessile or corymbose capitula 139
Leaves alternate, rarely opposite but then habit or capitula different 140

139 Leaves entire; capitula sessile ..... 8. **Asaemia**
Leaves pinnatifid; capitula corymbose ..... 5. **Gymnopentzia**

140 Capitula solitary or in lax to dense corymbs, small to medium-sized and generally erect; pollen usually spiny, rarely smooth (in *Ajaniopsis*, *Stilpnolepis*, *Filifolium*, and *Sphaeromeria*) ... 141
Capitula in elongated and paniculate, rarely racemiform or spiciform or subglobose inflorescences, often small and numerous and sometimes pendent; pollen smooth 168

141 Central floret corolla 4-lobed (rarely 3-lobed in *Cotula*) ... 142
Central floret corolla 5-lobed 150

142 Cypselas dorsiventrally flattened with 2 lateral more or less distinct ribs or wings 143
Cypselas not or only slightly dorsiventrally flattened without or with 3–5 ribs and no wings 146

143 Shrublets or half-shrubs with corymbose or occasionally solitary capitula ..... 106. **Schistostephium**
Annual or perennial herbs with solitary capitula, rarely few together 144

144 Capitula sessile; outer female florets without corolla and with style persistent and spinescent in fruit ..... 105. **Soliva**
Capitula more or less pedunculate; outer female florets with corolla; style not persistent 145

145 Outer female floret corolla inflated with a hollow space between the outer and inner layer; central florets female-sterile ..... 104. **Leptinella**
Outer female floret corolla not inflated; central florets generally fertile ..... 103. **Cotula**

146 Perennial (rarely facultative annual) prostrate herbs, regularly rooting at the nodes; central florets female-sterile ..... 104. **Leptinella**
Annual herbs, not regularly rooting at the nodes; central florets fertile 147

147 Disc corolla tube very much swollen and brittle ..... 88. **Oncosiphon**
Disc corolla tube not or only slightly swollen 148

148 Delicate, somewhat succulent herb; leaves with rounded lobes; capitula small, 5 mm or less in diam. ..... 58. **Nananthea**
Habit and leaves various; capitula generally more than 5 mm in diam. 149

149 Cypsela wall either white and spongy with 1 adaxial and 2 lateral weak ribs, abaxially thin, or cypselas almost terete and thin-walled all around (additional outer conspicuously rugose cypselas may be present) ..... 96. **Foveolina**
Cypsela wall not white and spongy, with 5 adaxial-lateral ribs ..... 92. **Matricaria**

150 Annual herbs 151
Perennial herbs or often half-shrubs, shrublets or shrubs . 156

151 Involucral bracts widely obovate and largely scarious; corolla limb inflated, crateriform; cypselas obovoid-lanceolate, densely glandular ..... 36. **Stilpnolepis**
Involucral bracts obovate-oblong, only marginally scarious; corolla limb more or less distinct but not inflated and crateriform; cypselas various but not obovoid-oblanceolate and densely glandular 152

152 Corolla lobes densely pilose; capitula few together in dense corymbs; cypselas obovoid with rows of myxogenic cells ..... 37. **Ajaniopsis**
Corolla lobes glabrous, sometimes glandular; capitula often solitary or laxly corymbose; cypselas various 153

153 Cypselas distinctly rugose to tuberculate, more or less 5-angled ..... 87. **Rennera**
Cypselas smooth or ribbed and not rugose to tuberculate (outer conspicuously rugose cypselas in addition to the smooth central cypselas sometimes present in *Foveolina*) 154

154 Cypselas somewhat dorsiventrally flattened and with 2 lateral weak ribs; corolla lobes with central resin sacs ..... 99. **Aaronsohnia**
Cypselas smooth and obovoid to terete, or with 3–5 adaxial-lateral, more or less distinct ribs; corolla lobes without or sometimes with central resin sacs (in *Matricaria*) 155

155 Cypsela wall either white and spongy with 1 adaxial and 2 lateral weak ribs, abaxially thin, or almost terete and thin-walled all around (additional outer conspicuously rugose cypselas may be present) ..... 96. **Foveolina**
Cypsela wall not white and spongy, with 5 adaxial-lateral ribs ..... 92. **Matricaria**

156 Cypselas dorsiventrally flattened, with or without lateral wings ..... 107. **Hippia**
Cypselas not dorsiventrally flattened, unwinged 157

157 Cypselas with dark vallecular secretory canals between the pale ribs and with myxogenic cells on the ribs .. 71. **Leucanthemum**
Cypselas with or without ribs but vallecular secretory canals absent 158

158 Capitula disciform; outer female florets present 159
Capitula discoid; all florets hermaphrodite 162

159 Central floret corollas soon compressed together in a resinous mass; cypselas obliquely obovoid; a perennial herb with basal fibrous leaf sheaths and filiform leaf lobes ..... 38. **Filifolium**
Central floret corollas not compressed in a resinous mass; cypselas straight and obovoid to obovate-oblong; habit and leaves various 160

160 Pollen smooth; small perennial herbs or half-shrubs ..... 39. **Sphaeromeria**
Pollen spiny (sometimes with short spines only); habit various 161

161 Style-branches brownish; corolla lobes erect . 35. **Phaeostigma**
Style-branches yellowish; corolla lobes spreading .. 34. **Ajania**

162 Cypselas slender and somewhat arcuate, tuberculate with numerous obtuse excrescences; a basally villous and woody perennial with much pinnatisect leaves and densely corymbose capitula ..... 27. **Pseudohandelia**
Cypselas obovoid-oblong, straight or somewhat oblique, smooth or ribbed but not tuberculate; habit, leaves and capitula various 163

163 Cypsela ribs acute, with secretory cavities (best seen in cross-section); corolla gradually expanded and funnel-shaped ..... 7. **Athanasia**
Cypsela ribs faint or rounded, without secretory cavities; corolla more or less distinctly divided into tube and limb 164

164 Cypselas 10–18-ribbed ..... 3. **Phymaspermum**

Cypselas with fewer than 10 ribs 165

165 Anthers tailed; perennial herbs with much pinnatisect, basally more or less rosulate leaves ..... 20. **Hippolytia**
Anthers not tailed; habit various; leaves entire or rather few-lobed 166

166 Perennial herbs with laxly corymbose capitula . 36. **Stilpnolepis**
Shrubs or shrublets with solitary capitula 167

167 Leaves with linear lobes ..... 30. **Brachanthemum**
Leaves ericoid with short lobes ..... 85. **Pentzia**

168 Capitula disciform; outer female florets present; involucral bracts in 2–5 rows 169
Capitula discoid; all florets hermaphrodite; involucral bracts in 4–7 rows, unequal, the outer short and rounded, the inner gradually longer and linear ..... 41. **Seriphidium**

169 Corolla lobes pilose 170
Corolla lobes glabrous, sometimes glandular 173

170 Cypselas densely pilose 171
Cypselas glabrous 172

171 Outer female florets without corolla and with dilated, lanceolate, flat style-branches; a virgate shrub ..... 46. **Mausolea**
Outer female florets with a tubular corolla and linear style-branches; a woody shrublet with older branches transformed into spines ..... 47. **Picrothamnus**

172 Leaves pinnatisect; capitula densely congested in glomerules arranged in spikes, or solitary in interrupted partly congested spikes; indumentum of simple of bifid hairs ..... 45. **Turaniphytum**
Leaves entire or few-lobed; capitula few in an elongated panicle, at the summit fasciculate; indumentum of stellate hairs ..... 40. **Kaschgaria**

173 Suffruticose perennial with entire or 3–5-lobed leaves; capitula 30–50-flowered in a pyramidal to elongated panicle (*Sphaeromeria ruthiae*) ..... 39. **Sphaeromeria**
Habit, leaves, and capitula various, usually with fewer than 30 florets 174

174 Central florets of two kinds; outer perfect, inner completely sterile with reduced ovaries; panicle spiciform; leaves pectinate-pinnatisect with filiform, apically somewhat swollen and mucronulate lobes ..... 44. **Neopallasia**
Central florets all perfect or all female-sterile with reduced ovaries; inflorescence and leaves various ..... 43. **Artemisia**

ANTHEMIDEAE Cass.

J. Phys. Chim. Hist nat. **88**: 192 (1819). Type species: *Anthemis maritima* L.

Aromatic annual or perennial herbs, subshrubs or shrubs, rarely spinescent. Leaves alternate or rarely opposite or fasciculate or rosulate, generally variously dissected, pinnatisect, pinnatifid, lobed or serrate-dentate or rarely entire. Capitula solitary or corymbose or paniculate, rarely aggregated, often pedunculate, sometimes sessile, variable in size, radiate or disciform and heterogamous or homogamous and discoid. Involucral bracts in three or more rows, rarely in two rows, imbricate, almost always with scarious margins and apex. Receptacle paleate or epaleate, rarely pilose or hirsute. Ray florets (in radiate capitula) female, fertile or sterile, or neuter; limb white, yellow or rarely blue-violet, pink or reddish. Outer female florets (in disciform capitula) in one or more rows, tubular, rarely without corollas. Central disc florets 5- or 4-lobed, rarely 3-lobed, yellow or rarely whitish or red, rarely somewhat zygomorphic, perfect or functionally male. Anthers generally obtuse at base, rarely shortly tailed; filaments basifixed. Style-branches (in central florets) almost always truncate and penicillate, with stigmatic areas in two marginal stripes, but sometimes undivided in functionally staminate florets. Cypselas variable, homo- or heteromorphic, generally terete to weakly angled or ribbed or flattened, sometimes winged, thin- or thick-walled, without a carbonized layer, often with secretory canals and myxogenic cells. Pappus generally of rather few scarious scales, a corona or an auricle, rarely of many flat bristle-like scales, often absent. Embryo sac monosporic or sometimes tetrasporic, rarely bisporic. Chromosome number generally x=9, sometimes x=10, rarely x=6, 7, 8, 11 or 18. Irregular monoterpenes present in high concentrations.

DISTRIBUTION (Table 3). Worldwide but with main concentrations in central Asia, the Mediterranean region and South Africa. – 12 subtribes, 108 genera, 1741 spp.

The interrelationships of the 12 proposed subtribes are uncertain, but one possible hypothesis is presented in the cladogram (Fig. 1). It should be noted that a number of equally parsimonious solutions are possible, and that the strict consensus tree of these solutions is totally collapsed. The chosen cladogram is offered simply as a suggestion for further analysis and test. The characters used to identify the various clades, indicated in the cladogram, are listed with comments below.

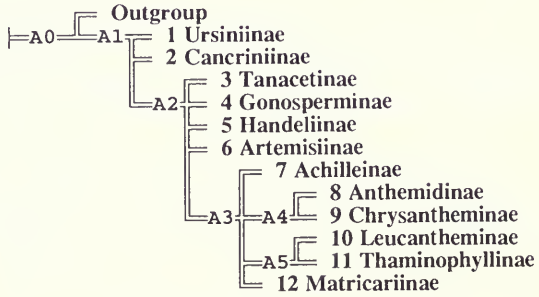

Fig. 1 Cladogram (of five possible) of the 12 subtribes; produced by the *mhennig** option in Hennig86. Cladogram length = 39, consistency index = 84, retention index = 53.

Clades and characters – Fig. 1, Tables 2 & 4.

Clade AO

15 *Leaves variously deeply lobed or divided.* Dissected leaves are characteristic of most Anthemideae as well as of its postulated relatives in the Heliantheae. Some of the Anthemideae genera and species have entire leaves, but these taxa are clearly related to other taxa with dissected leaves.

43 *Involucral bracts with scarious margins.* This is characteristic of almost all Anthemideae as well as of its postulated relatives in Heliantheae, but also in some austral and grangeoid Astereae. At the generic level. *Myxopappus* with subulate involucral bracts represents a reversal.

Clade A1 – tribe Anthemideae

Table 4 Data matrix for the Anthemideae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	111 1 1 1 1 11 1 111 1450574597 4616 1319758857 422746 5327185659441928651321242511101706
1. Ursiniinae	a1aa1?a11100p0000p00pp00p0pp00000
2. Cancriniinae	a1aa1?0000aap0000p000p000?0000000
3. Tanacetinae	a1aa1ap000pp1pppppp0pp000pp00p00p
4. Gonosperminae	a1aa1?a0p0001a100p0000000?0000000
5. Handeliinae	a1?a1?p000001001a100pp000?0000000
6. Artemisiinae	a1aa1ap000pp1000ppa1ap0000p000000
7. Achilleinae	a1aa1aa0000p1000ppp0aaa100pp0p000
8. Anthemidinae	a1aa1ap0000p10000pp0pap0a1p00000p
9. Chrysantheminae	a1aa1?0000001000p0001a001pa11p000
10. Leucantheminae	a1a11?p0000p10000pa0pap000pp0a00p
11. Thaminophyllinae	a1a11?pp00001000000pp000?000a100
12. Matricariinae	aaa11ap0p0001000pp00pap00ppp00paa

52 *Ray floret limb white.* Rays in the Anthemideae are mostly white and sometimes yellow (rarely pink, reddish or blue-violet). In the Heliantheae relatives rays are yellow.

107 *Cypselas terete to weakly angled, or flattened.* The fruits are very variable in the Anthemideae, but the sharply angled type, present in all of its postulated immediate relatives in the Heliantheae, is hardly ever present.

151 *Cypsela wall without carbonized layer.* A carbonized layer in the fruit wall is characteristic of many Heliantheae and of all Eupatorieae, including the immediate relatives of the Anthemideae, but it is totally absent in this tribe. The absence of this feature is thus interpreted as a derived condition for the tribe.

178 *'Irregular' monoterpenes in high concentrations present* (Greger, 1977).

Clade A2

161 *Pappus of short (not large and obovate or bristle-like) scales, an auricle, a corona, or absent.* In subtribe Cancriniinae, which is not a member of this clade, the pappus consists of many subulate, bristle-like scales and it looks very anomalous within the tribe. The same pappus type is found in the immediate relatives within Heliantheae. *Ursinia* in subtribe Ursiniinae, also not a member of this clade, has a pappus of large and obovate scales, similar to some of the wider pappus scales in Cancriniinae and Heliantheae. Judging from other characters, *Ursinia* is related to a number of South African genera, all united in subtribe Ursiniinae. In these genera the pappus is absent and we consider it secondarily lost. However, in one genus, *Hymenolepis*, a pappus of small scales has evolved. In all other Anthemideae, comprising clade A2 and excluding Cancriniinae and Ursiniinae, the pappus, if not secondarily lost, consists of scales, an auricle or a corona.

Clade A3

51 *Floral parts with resin canals.* Resin canals or sacs are frequently present in style-branches, corolla lobes and sometimes also anther tips in a majority of the Anthemideae. They seem to occur mainly in the subtribes of this clade, though present also in some genera of other subtribes.

Clade A4

152 *Cypsela wall several cell layers thick, partially or completely sclerified.*

Clade A5

21 *Leaves serrate-dentate.* In the two subtribes of this clade non-dissected leaves dominate, though there are exceptions in several genera.

1. URSINIINAE Bremer & Humphries, subtrib. nov.

Type species: *Ursinia paradoxa* Gaertner (*U. chrysanthemoides* (Less.) Harvey).

Herbae annuae vel perennes vel frutices. Corollae flosculorum radii cellulis epidermalibus tabularibus. Antherae cellulis endothecii polaratis. Pappus squamiformis magnus aut parvus vel nullus. Furanosesquiterpena adsunt.

Annual or perennial herbs or shrubs. Leaves alternate or sometimes opposite, variable in shape. Capitula solitary or laxly to densely corymbose, pedunculate or rarely sessile along the stems, radiate or discoid. Receptacle paleate or epaleate. Ray floret limb yellow, white or rarely red; epidermis cells tabular. Disc corolla 5-lobed. Anthers with endothecial tissue polarized. Cypselas 5- to many-ribbed, glabrous or pubescent, papillose to copiously villous, sometimes with myxogenic cells. Pappus of large or small scales, or often absent. Furanosesquiterpenes present.

DISTRIBUTION (Table 5). Southern Africa, one *Ursinia* species in Ethiopia and one *Lasiospermum* species in Egypt (Sinai), some *Ursinia* species introduced in Australia and New Zealand. – 8 genera, 114 spp.

Table 5 General distribution of Ursiniinae and genera. x=indigenous, o=introduced.

	S. Eur.	N. Afr.	S. Afr.	Austr. N. Zeal.
Ursiniinae	o	x	x	o
Ursinia		x	x	o
Lasiospermum		x	x	
Phymaspermum			x	
Eumorphia			x	
Gymnopentzia			x	
Hymenolepis			x	
Athanasia			x	
Asaemia			x	

This subtribe was first identified as a group by Bohlmann and collaborators (Greger, 1977), who discovered that a number of South African Anthemideae genera contained furanosesquiterpenes rather than the common polyacetylenes. Subsequently, the classification of the group has been revised by Källersjö (1986, 1991), who added a number of micromorphological characters (see cladogram in Fig. 2). Källersjö circumscribed it more precisely, by moving a number of *Athanasia* species (to *Inulanthera* in the Gonosperminae) and by including some chemically unknown genera, now placed in *Phymaspermum* and *Hymenolepis*, which have now been investigated chemically. The tribal position of *Ursinia* within Anthemideae, discussed below, has gained further support.

There is one alternative equally parsimonious cladogram to that shown here. In the alternative cladogram *Phymaspermum* and *Gymnopentzia* are sister groups based on a shared loss of receptacular paleae (character 45), whereas in the presented cladogram *Gymnopentzia* and *Eumorphia* are sister groups based on their opposite leaves (character 14).

Clades and characters – Fig. 2, Tables 2, 6.

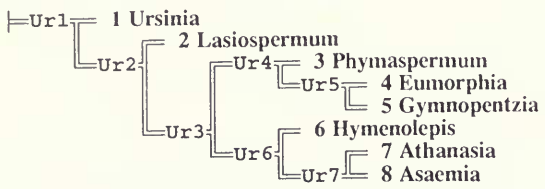

Fig. 2 Cladogram (of two possible) of the Ursiniinae produced by the *ie* option in Hennig86. Cladogram length = 39, consistency index = 82, retention index = 79.

Table 6 Data matrix for the Ursiniinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	111 1111111 111 1 1 11 1 1 145057 4597566735 2224413415673956822 31 532718 5659941230289454456219424209 6344
1. *Ursinia*	11aa1? 1111110p000000000p00000000000000
2. *Lasiospermum*	11111? 11110011110000000p00000000000000
3. *Phymaspermum*	a1111? 011100110011a11a0p000000000000p0
4. *Eumorphia*	a1111? a1110 0110011a110a00000000000000
5. *Gymnopentzia*	11?11? 0?1100110011111011100000000000000
6. *Hymenolepis*	a1?11? a?1100100011000010111 110000000
7. *Athanasia*	a1?11? a?1100110011a00001011111a11a1000
8. *Asaemia*	01?11? 0?1100110011000011 0?111111100111

	1111 11 1 177675555566666171 240 337 356600357905678511121997853
1. *Ursinia*	???000000000000000pppp00000
2. *Lasiospermum*	?00??0000000000000p00000000
3. *Phymaspermum*	??????000000000000000000000
4. *Eumorphia*	?????000000000000000000000
5. *Gymnopentzia*	????????????????????0000000000
6. *Hymenolepis*	???000???????????00000p0000
7. *Athanasia*	?????0???????????00p00pppp0
8. *Asaemia*	????????????????????00000000p

Clade Ur1 – subtribe Ursiniinae

45 *Receptacle paleate.* The distribution of this character is difficult to interpret. Receptacular paleae are absent in *Phymaspermum*, *Gymnopentzia*, *Asaemia*, a few species of *Athanasia*, and one species of *Hymenolepis*. This is most parsimoniously interpreted as secondary losses within the subtribe.

56 *Ray floret limb epidermis cells tabular (senecioid or mutisioid type)* (Baagøe, 1977).

95 *Anthers with endothecial tissue partly or wholly polarized.*

179 *Furanosesquiterpenes present.*

Ursinia

159 *Cypsela wall with a continuous ring of fibre-like cells.*

164 *Pappus of 5 convolute-contorted scales.*

Clade Ur2

161 *Pappus of short (not large and obovate or bristle-like) scales, an auricle, a corona, or absent.*

172 *Pappus absent in ray and disc cypselas. Hymenolepis* has a pappus of small scales, most parsimoniously interpreted as secondarily evolved within this clade.

Lasiospermum

133 *Cypselas with costal resin canals or sacs.* These structures are similar to those occurring in the subtribe Matricariinae, for example, but different from those in *Hymenolepis*, *Athanasia*, and *Asaemia* (character 132).

150 *Cypselas copiously villous, seemingly covered in 'cotton wool'.*

Clade Ur3

2 *Plants shrubby.*

28 *Leaves with secretory cavities.*

29 *Capitula densely corymbose. Asaemia* and some species of *Athanasia* and *Phymaspermum* have solitary capitula.

Clade Ur4

124 *Cypselas with 10 (8–12) multicellular epicarpic ribs.* Occasionally there are up to 18 ribs.

145 *Cypselas papillose.*

Phymaspermum

45 reversed. See clade Ur1.

144 *Cypselas with scattered, ovoid, myxogenic trichomes.* In a few species the trichomes are not myxogenic, though similar in structure.

Clade Ur5

14 *Leaves opposite.*

Eumorphia

There is no autapomorphy for *Eumorphia*. The matter is further discussed under the genus.

Gymnopentzia

35 *Capitula discoid.*

45 reversed. See clade Ur1.

146 *Cypselas long-papillose, seemingly pubescent.*

Clade Ur6

12 *Plants with stellate hairs.*

35 *Capitula discoid.*

51 *Floral parts with resin canals.*

69 *Corolla gradually expanded, rather thin and funnel-shaped.*

74 *Corollas with continuous veins extending into the lobes.*

132 *Cypsela ribs with ellipsoid secretory cavities forming longitudinal ducts.*

Hymenolepis

172 reversed. See clade Ur2.

Clade Ur7

94 *Anthers with an apical resin sac.* This character occurs in most but not all species of *Athanasia*.

152 *Cypsela wall several cell layers thick, partially or completely sclerified.*

160 *Cypsela wall with a continuous ring of sclerified isodiametric cells.*

Athanasia

89 *Corolla tube with long-stalked glands; stalk cells elongated.* Some species of *Athanasia* have glabrous corolla tubes, apparently secondarily.

126 *Cypsela ribs protruding, narrow and somewhat wing-like.*

Asaemia

14 *Leaves opposite.*

15 reversed. *Leaves not variously deeply lobed or divided, but entire.*

23 *Leaves entire, ericoid.*

29 reversed. See clade Ur3.

34 *Capitula sessile along the stems.*

45 reversed. See clade Ur1.

114 *Cypselas dorsiventrally flattened.*

1. **URSINIA** Gaertner, *Fruct. sem. pl.* **2**: 462 (1791). Type species: *U. paradoxa* Gaertner (*U. chrysanthemoides* (Less.) Harvey). – *Sphenogyne* R. Br. – *Ursiniopsis* E. Phillips.

Annual or perennial herbs or shrublets. Leaves alternate, entire or generally variously lobed. Capitula solitary or laxly corymbose, pedunculate, radiate or occasionally discoid. Receptacle paleate; paleae scarious, often enveloping florets, sometimes narrow with an apical limb. Ray florets generally neuter or occasionally female, sterile or fertile; limb yellow, white, or rarely red, dorsally often reddish; epidermis cells tabular. Disc corolla shallowly 5-lobed. Anthers with a widely ovate apical appendage; endothecial tissue polarized. Cypselas slender or obovoid, straight or curved, 5-ribbed, with a basal tuft of long hairs or glabrous. Pappus of 5 (rarely 8–10) large, convolute-contorted, whitish scales, or of 5 outer such scales and 5 inner subulate, whitish scales, or occasionally absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa mainly in the SW Cape, also in Namibia, Botswana, and Ethiopia. – 38 spp.

Ursinia was revised by Prassler (1967). Species without a basal tuft of cypsela hairs earlier constituted *Ursinia* s. s. (excluding *Sphenogyne*; the two genera differed also in other characters). Species with glabrous cypselas are considered derived by Prassler so we assume that presence of cypsela hairs is a diagnostic character for the whole genus, though secondarily lost in some species. Another former genus, *Ursiniopsis*, was distinguished simply by female rather than neutral rays. It was reduced to synonomy by Prassler. Earlier authors, e.g. Bentham (1873a), placed *Ursinia* in the tribe Arctoteae sensu Norlindh (1977) mainly because of its well developed pappus scales. Cassini (1816) followed by Beauverd (1915) and Prassler considered it a member of Anthemideae. Robinson & Brettell (1973) argue that inclusion in the Anthemideae of the anomalous genus *Ursinia* with its conspicuous pappus scales, widely ovate apical anther appendages, and different pollen (exine without columnar structure) would destroy a workable tribal concept. Hence they proposed a monotypic new tribe, Ursinieae. The large pappus scales and the shape of the apical anther appendage may be plesiomorphies within Anthemideae, since similar structures occur in the outgroup. The pollen was investigated by Stix (1960) and she concluded that *Ursinia* belongs in Anthemideae. The presence of unique furanosesquiterpenes in *Ursinia* and a number of other South African Anthemideae corroborates its tribal position.

Although mainly South African, there is one species (*U. nana*) also known from Ethiopia and *U. anthemoides* is introduced into western Australia. The following list of species is taken mainly from Prassler's revision.

U. abrotanifolia (R. Br.) Sprengel
U. anethoides (DC.) N. E. Br.
U. anthemoides (L.) Poiret
U. brachyloba (Kunze) Bremer & Humphries, **comb. nov.** Basionym: *Sphenogyne brachyloba* Kunze in *Linnaea* **20:** 21 (1847).
U. cakilefolia DC.
U. caledonica (E. Phillips) Prassler
U. calenduliflora (DC.) N. E. Br.
U. chrysanthemoides (Less.) Harvey (*U. paradoxa* Gaertner)
U. coronopifolia (Less.) N. E. Br.
U. dentata (L.) Poiret
U. discolor (DC.) N. E. Br.
U. dregeana (DC.) N. E. Br.
U. eckloniana (Sonder) N. E. Br.
U. filipes (E. Meyer ex DC.) N. E. Br.
U. frutescens Dinter
U. heterodonta (DC.) N. E. Br.
U. hispida (DC.) N. E. Br.
U. macropoda (DC.) N. E. Br.
U. merxmuelleri Prassler
U. montana DC.
U. nana DC.
U. nudicaulis (Thunb.) N. E. Br.
U. oreogena Schltr ex Prassler
U. paleacea (L.) Moench (*U. crithmoides* (P. Bergius) Poiret)
U. pilifera (P. Bergius) Poiret
U. pinnata (Thunb.) Prassler
U. punctata (Thunb.) N. E. Br.
U. pygmaea DC.
U. quinquepartita (DC.) N. E. Br.
U. rigidula (DC.) N. E. Br.
U. saxatilis N. E. Br.
U. scariosa (Aiton) Poiret
U. sericea (Thunb.) N. E. Br.
U. serrata (L. f.) Poiret
U. speciosa DC.
U. subflosculosa (DC.) Prassler
U. tenuifolia (L.) Poiret
U. trifida (Thunb.) N. E. Br.

2. **LASIOSPERMUM** Lagasca, *Gen. sp. pl.*: 31 (1816). Type species: *L. pedunculare* Lagasca (*L. erectum* (Lam.) Druce).

Annual or perennial herbs. Leaves alternate, variously pinnatisect. Capitula solitary, pedunculate, radiate or discoid. Receptacle flat or convex, paleate; paleae thin and scarious with a conspicuous resin canal. Ray florets female, fertile; limb very short to long, white or reddish; epidermis cells tabular. Disc corolla 5-lobed; lobes sometimes reddish. Anthers with endothecial tissue polarized. Cypselas copiously villous, with resin canals. Pappus absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the Cape, Namibia, and Egypt in Sinai. – 4 spp.

Lasiospermum is a well defined genus with copiously villous cypselas and the development of the cypsela wool deserves detailed investigation. One annual species (*L. brachyglossum*) occurs also in Sinai. Similar disjunctions are known also from other groups. The first three species in the list are taken from *Flora capensis* (Harvey, 1865).

L. bipinnatum (Thunb.) Druce (*L. radiatum* Trevir.)
L. brachyglossum DC.
L. erectum (Lam.) Druce (*L. pedunculare* Lagasca)
L. poterioides Hutch. – *Note:* Description in Hutchinson, 1946.

3. **PHYMASPERMUM** Less., *Syn. gen. compos.*: 253 (1832). Type species: *P. junceum* Less. – *Adenachaena* DC. – *Brachymeris* DC. – *Iocaste* E. Meyer ex Harvey

Shrubs or half-shrubs. Leaves alternate, entire or lobed, often ericoid with secretory cavities. Capitula solitary or corymbose, generally pedunculate, rarely sessile along the stems, radiate or discoid. Receptacle flat to conical, epaleate. Ray florets female, fertile; limb white; epidermis cells tabular. Disc corolla 5-lobed, rarely pubescent with long hairs, with a narrow tube and a distinct limb. Cypselas 10-18-ribbed, generally minutely papillose especially on the ribs and generally with scattered ovoid myxogenic trichomes, with a more or less distinct apical rim. Pappus absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the Cape, Orange Free State, and Transvaal, Swaziland, Zimbabwe and Namibia. – 18 spp.

Phymaspermum was formerly diagnosed as South African shrubs with epaleate and radiate capitula and papillose and glandular cypselas. Only the cypsela character represents a useful synapomorphy for the genus. *Phymaspermum* cypselas have a peculiar and unique type of myxogenic trichome, which are ovoid or almost subglobose and scattered over the cypsela surface. *Brachymeris* was first described as a monotypic genus and the type species, *B. scoparia*, is a shrub with much reduced leaves, small capitula sessile along the stems, and a pubescent corolla. Hutchinson (1917) described four new species and transferred one *Pentzia* species to *Brachymeris*, mainly because they all, like *B. scoparia*, possessed cypselas without a pappus. Hutchinson's species differ from *B. scoparia* in several characters; they have rather closely set long leaves, capitula in corymbs, and glandular but not pubescent corollas. Källersjö (1986), who investigated these genera, concluded that *B. scoparia* as well as Hutchinson's species could be transferred to *Phymaspermum* because of their similar cypsela morphology. All *Brachymeris* species have the *Phymaspermum* type of ovoid cypsela trichomes, although they are not always myxogenic. Källersjö also transferred a group of *Athanasia* species with the same cypsela morphology to *Phymaspermum*. These *Athanasia* species are also in habit similar to *P. aciculare* for example. The species of *Phymaspermum* s. s. (excluding the former *Athanasia* and *Brachymeris* species but including *Adenachaena* and *Iocaste*) are taken from *Flora capensis* (Harvey, 1865) with three species described later added. The former *Athanasia* and *Brachymeris* species are best identified using the treatments by Hilliard (1977) and Hutchinson (1917), respectively.

P. acerosum (DC.) Källersjö (*Athanasia acerosa* (DC.) D. Dietr.
P. aciculare (E. Meyer ex Harvey) Benth. ex B. D. Jackson (*Iocaste acicularis* E. Meyer ex Harvey)
P. appressum Bolus – *Note:* Description in Bolus, 1905.
P. argenteum Brusse – *Note:* Description in Brusse, 1989*b*.
P. athanasioides (S. Moore) Källersjö (*Brachymeris athanasioides* (S. Moore) Hutch.)
P. bolusii (Hutch.) Källersjö (*Brachymeris bolusii* Hutch.)
**P. equisetoides* Thell. – *Note:* Description in Thellung, 1923.
P. erubescens (Hutch.) Källersjö (*Brachymeris erubescens* Hutch.)
P. junceum Less.
P. leptophyllum (DC.) Benth. ex B. D. Jackson (*Adenachaena leptophylla* DC.)
P. montanum (Hutch.) Källersjö (*Brachymeris montana* Hutch.)
P. parvifolium (DC.) Benth. ex B. D. Jackson (*Adenachaena parvifolia* DC.)
P. peglerae (Hutch.) Källersjö (*Brachymeris peglerae* Hutch.)
P. pinnatifidum (Oliver) Källersjö (*Athanasia pinnatifida* (Oliver) Hilliard)
P. schroteri Compton – *Note:* Description in Compton, 1931.
P. scoparium (DC.) Källersjö (*Brachymeris scoparia* DC.)
P. villosum (Hilliard) Källersjö (*Athanasia villosa* Hilliard)
P. woodii (Thell.) Källersjö – *Athanasia woodii* (Thell.) Hilliard)

4. **EUMORPHIA** DC., *Prodr.* **6**: 2 (1838). Type species: *E. dregeana* DC.

Shrubs. Leaves opposite, rarely alternate, entire or lobed, more or less ericoid, with secretory cavities. Capitula generally solitary or corymbose, generally pedunculate, radiate. Receptacle flat or slightly convex, rarely conical, generally paleate, sometimes epaleate. Ray florets female, fertile; limb white; epidermis cells tabular. Disc corolla 5-lobed, with a narrow tube and a distinct limb. Anthers with endothecial tissue polarized. Cypselas 10–12-ribbed, rarely up to 18–ribbed, minutely papillose especially on the ribs, with an apical rim. Pappus absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the central Cape, Natal and Transvaal, and in Lesotho and Swaziland. – 6 spp.

Traditionally *Eumorphia* comprises South African Anthemideae with radiate capitula (a plesiomorphy), a paleate receptacle and cypselas without a pappus, characters common to several other genera. *E. prostrata* has a partly

epaleate receptacle. The apical cypsela rim present in *Eumorphia* occurs also in other genera, e.g. *Phymaspermum*. *Eumorphia* has opposite leaves, which also characterize *Gymnopentzia*. One species, *E. davyi*, is aberrant in having alternate, closely set leaves and a conical receptacle. It is provisionally retained in *Eumorphia* by Källersjö (1985). The circumscription of this genus obviously needs further consideration.

E. corymbosa E. Phillips – *Note:* Description in Phillips, 1950.
E. davyi Bolus – *Note:* Description in Bolus, 1906.
E. dregeana DC. – *Note:* Description in Harvey, 1865.
E. prostrata Bolus – *Note:* Description in Hilliard, 1977.
E. sericea J. M. Wood & M. Evans – *Note:* Description in Hilliard, 1977.
E. swaziensis Compton – *Note:* Description in Compton, 1976.

5. **GYMNOPENTZIA** Benth. in Benth. & Hook. f., *Gen. pl.* **2**(1): 537 (1873). Type species: *G. bifurcata* Benth.

A shrub. Leaves opposite, pinnatifid, somewhat ericoid, with secretory cavities. Capitula corymbose, discoid. Receptacle flat or slightly convex, epaleate. Corolla 5-lobed, with a narrow tube and a distinct limb. Anthers with endothecial tissue polarized. Cypselas 10-ribbed, densely long-papillose and thus seemingly pubescent. Pappus absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the E. Cape, Natal and Transvaal, and in Lesotho. – Monotypic.

In related genera, i. e. *Eumorphia* and *Phymaspermum*, the cypselas are minutely papillose, the epidermis cells being more or less projected. This is especially pronounced in *Gymnopentzia*, the papillae often being much longer than wide and similar to unicellular hairs. The cypselas are thus often described as pubescent. The opposite leaves is another distinguishing feature from *Phymaspermum* and possibly synapomorphic with *Eumorphia*.

6. **HYMENOLEPIS** Cass. in *Bull. Sci. Soc. philom. Paris* **1817**: 138 (1817). Type species: *H. parviflora* (L.) DC. – *Phaeocephalus* S. Moore.

Pubescent shrubs; hairs stellate. Leaves alternate, lobed, serrate-dentate or entire, with secretory cavities. Capitula slender, few-flowered, corymbose, sometimes rather densely aggregated, discoid. Receptacle flat, generally paleate, rarely epaleate. Corolla gradually expanded and funnel-shaped, 5-lobed, with short-stalked glands and with continuous veins also in the lobes. Anthers with endothecial tissue polarized. Cypselas 5–10-ribbed, with ellipsoid secretory cavities forming longitudinal ducts. Pappus a corona of fimbriate scales. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the Cape. – 7 spp.

Harvey's (1865) treatment of *Hymenolepis* as a separate genus rather than as a section of *Athanasia* was recently revived by Källersjö (1986), since *Athanasia* including *Hymenolepis* is paraphyletic. *Athanasia* s. s. is more closely related to *Asaemia* than to *Hymenolepis*, as shown in the cladogram (Fig. 2). *Hymenolepis* differs by its slender, few-flowered capitula and scaly pappus. The monotypic *Phaeocephalus* was reduced to a synonym of this genus by Källersjö. A key to the species was provided by Bremer & Källersjö (1986).

H. cynopus Bremer & Källersjö
H. dentata (DC.) Källersjö (*Athanasia schizolepis* Harvey)
H. gnidioides (S. Moore) Källersjö (*Phaeocephalus gnidioides* S. Moore)
H. incisa DC.
H. indivisa (Harvey) Källersjö
H. parviflora (L.) DC.
H. speciosa (Hutch.) Källersjö

7. **ATHANASIA** L., *Sp. pl.* 2nd ed.: 1180 (1763). Type species: *A. crithmifolia* (L.) L. (Bremer & Wijnands, 1982). – *Stilpnophyton* Less.

Glabrous or pubescent shrubs; hairs stellate. Leaves alternate, entire, dentate, or lobed, generally ericoid, with secretory cavities. Capitula generally corymbose, more rarely solitary, discoid. Receptacle flat, generally paleate, rarely epaleate. Corolla gradually expanded and funnel-shaped, 5-lobed, glabrous or with long-stalked glands, with continuous veins also in the lobes. Anthers often with an apical resin sac; endothecial tissue polarized. Cypselas 5–12-ribbed generally with protruding and narrow ribs, glabrous or occasionally glandular, with ellipsoid secretory cavities forming longitudinal ducts. Pappus absent or often a pseudopappus of stalked glands. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa, mainly in the SW Cape, one species in Natal (*A. grandiceps*). – 39 spp.

Athanasia traditionally embraced all South African, discoid Anthemideae with a paleate receptacle. Epaleate species were placed in other genera, e. g. *Pentzia* and *Stilpnophyton*. *Athanasia* and *Stilpnophyton* (as well as *Asaemia*) have similar cypsela wall anatomy, with a continuous ring of sclerified isodiametric cells. *Stilpnophyton* was reduced to a synonym by Källersjö (1986).

Several former species of *Athanasia* have now been transferred by Källersjö to the genera *Hymenolepis*, *Phymaspermum*, and *Inulanthera*. The remaining part, *Athanasia* s. s. is a homogeneous and monophyletic group. Characteristically, the cypsela ribs are narrow and somewhat wing-like, and the cypselas are often furnished with a peculiar 'pseudopappus' of long-stalked glands. In some species such glands are also present on the corolla tube, and in others they are totally absent, probably secondarily. In her most recent treatment of *Athanasia* (Källersjö, 1991) the distinctive characters of *Asaemia* are considered to be autapomorphic and *A. minuta* is considered to be very similar to *Athanasia humilis* Källersjö. The list of species is based on Källersjö (1986, 1991).

A. adenantha (Harvey) Källersjö
A. alba Källersjö
A. bremeri Källersjö
A. calophylla Källersjö
A. capitata (L.) L.
A. cochlearifolia Källersjö
A. crenata (L.) L.
A. crithmifolia (L.) L.
A. cuneifolia Lam.
A. dentata (L.) L.

A. elsiae Källersjö
A. filiformis L. f.
A. flexuosa Thunb.
A. grandiceps Hilliard & Burtt
A. hirsuta Thunb.
A. humilis Källersjö
A. imbricata Harvey
A. inopinata (Hutch.) Källersjö (*Stilpnophyton inopinatum* Hutch.)
A. juncea (DC.) D. Dietr.
A. leptocephala Källersjö
A. linifolia Burm. (*Stilpnophyton linifolium* (L. f.) Less., *Stilpnophyton longifolium* (Thunb.) Less.)
A. microcephala DC.
A. microphylla DC.
A. minuta (L. f.) Källersjö
A. oocephala (DC.) Källersjö (*Stilpnophyton oocephalum* DC.)
A. pachycephala DC.
A. pectinata L. f.
A. pinnata L. f.
A. pubescens (L.) L.
A. quinquedentata Thunb.
A. rugulosa E. Meyer ex DC.
A. scabra Thunb.
A. sertulifera DC.
A. spathulata (DC.) D. Dietr.
A. tomentosa Thunb.
A. trifurcata (L.) L.
A. vestita (Thunb.) Druce
A. virgata Jacq.
A. viridis Källersjö

8. **ASAEMIA** (Harvey) Harvey ex Benth. in Benth. & Hook. f., *Gen. pl.* **2**(1): 433 (1873). Type species: *A. axillaris* (Thunb.) Harvey ex Hoffmann (*A. minuta* (L. f.) Bremer).

A glabrous, sometimes spiny shrub. Leaves opposite, sheathing, entire, ericoid, with secretory cavites. Capitula sessile, solitary along the branches and on lateral branchlets, discoid. Receptacle flat, epaleate. Corolla gradually expanded and funnel-shaped, 5-lobed, glandular, with continuous veins also in the lobes. Anthers with an apical resin sac; endothecial tissue polarized. Cypselas 2–5-angled but generally dorsiventrally flattened with 1 adaxial and 2 lateral ribs, glabrous or basally with a few hairs, with few ellipsoid secretory cavities forming longitudinal ducts, apically with a smooth or denticulate thickened rim. Pappus absent. Furanosesquiterpenes present.

DISTRIBUTION. S. Africa in the Cape and in Namibia. – Monotypic.

Asaemia minuta is habitually very distinct, a shrub with ericoid leaves and small sessile capitula. It is sometimes spinescent (ssp. *minuta*) and sometimes unarmed (ssp. *inermis* (E. Phillips) Bremer). *Asaemia* is related to *Athanasia*. They have similar cypsela wall anatomy with a continuous ring of sclerified isodiametric cells (Källersjö, 1986). Both *Asaemia* and most species of *Athanasia* also have anthers with apical resin sacs. The genus was revised by Bremer (1983) but sunk into *Athanasia* by Källersjö (1991).

2. **CANCRINIINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Cancrinia chrysocephala* Karelin & Kir.

Plantae perennes, herbaceae vel suffruticosae, compactae, plusminusve scaphoideae. Bracteae involucri plerumque margine atrofuscae. Pappus e squamis vel setis planis pluribus, obovatis vel linearibus, albidis vel brunneis, longitudine quam corolla 2-plo brevioribus vel longioribus formatus.

Compact, more or less scaphoid perennial herbs or half-shrubs. Leaves alternate to rosulate, pinnatifid to pinnatisect. Capitula solitary, pedunculate, radiate or discoid. Involucral bracts generally with dark brown margins. Receptacle epaleate, glabrous or sometimes pilose or hirsute. Ray floret limb white, yellow, pinkish or bluish violet. Disc corolla 5-lobed, sometimes pilose. Cypselas 5–15-ribbed, glabrous or pilose. Pappus of several, obovate to linear, whitish or brownish scales or flat bristles, at least half as long as the corolla.

DISTRIBUTION (Table 7). Asia, mainly central part. – 6 genera, 26 spp.

Table 7 General distribution of Cancriniinae and genera. x=indigenous, o=introduced.

	C.& E. Asia	SW Asia
Cancriniinae	x	x
Trichanthemis	x	
Ugamia	x	
Richteria	x	x
Allardia	x	
Cancrinia	x	
Cancriniella	x	

This subtribe comprises some of the most plesiomorphic representatives of the tribe Anthemideae. In habit species of *Trichanthemis* and *Richteria*, and in pappus structure *Ugamia* and *Allardia*, are similar to members of the outgroup in tribe Heliantheae. Most species are restricted to mountain habitats in central Asia. *Ugamia*, *Cancriniella* and some *Trichanthemis* species, are small, compact, much woody, cushion-formed half-shrubs. *Cancrinia* and *Allardia* are compact perennial herbs. This habit character, together with the dark brown-margined involucral bracts, are both considered synapomorphies for the genera of the subtribe. It is possible that groups of species in *Tanacetum*, subtribe 'Tanacetinae', also sharing these features, are related to members of Cancriniinae rather than 'Tanacetinae', and should be transferred to Cancriniinae.

The cladogram for the genera is only one of several equally parsimonious ones, and shown only to display one possible hypothesis of generic interrelationships. The strict consensus tree for the alternative cladograms is totally collapsed.

Clades and characters – Fig. 3, Tables 2, 8.

Clade Ca1 – subtribe Cancriniinae

4 *Plants compact and more or less scaphoid. Allardia* and *Cancrinia* are compact, more herbaceous perennials with rather short peduncles, whereas the other genera are much

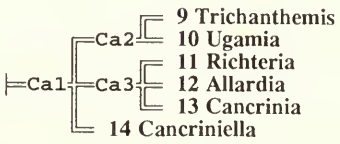

Fig. 3. Cladogram (of 21 possible) of the Cancriniinae produced by the *ie* option in Hennig86. Cladogram length = 14, consistency index = 85, retention index = 60.

Table 8 Data matrix for the Cancriniinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	111	1	1	1	11	11
	145057	44483375346			15775555566666175	
	532718	447983504981			30563567905678511	
9. *Trichanthemis*	11a11?	1a11a0p00000			????000000000000p	
10. *Ugamia*	a1?a1?	a11001100000			????????????????0	
11. *Richteria*	a1aa1?	a10000010000			????000000000000p	
12. *Allardia*	a1aa1?	a10000011000			????0000000000000	
13. *Cancrinia*	a1?a1?	a10000110000			????????????????p	
14. *Cancriniella*	a1?a1?	a10000100111			????????????????0	

woody basally, generally with long peduncles. *Ugamia* has short peduncles.

44 *Involucral bracts with dark brown margins.* This character is absent in some *Trichanthemis* species.

Clade Ca2

147 *Cypselas densely pilose; hairs subulate, with a few basal cells and one long apical cell. Cancrinia* and some species of *Allardia* sometimes have sparsely pilose cypselas.

Trichanthemis

49 *Receptacle densely hirsute.*

88 *Disc corolla tube pilose.* Some species of *Trichanthemis* have glabrous corollas.

Ugamia

33 *Capitula on short and nodding peduncles.*

35 *Capitula discoid.* Some species of *Trichanthemis*, *Cancrinia* and *Cancriniella* are also discoid.

Clade Ca3

170 *Pappus scales brownish.*

Richteria

There is no obvious autapomorphy for this genus, and it appears undefined compared to *Allardia* and *Cancrinia*.

Allardia

54 *Ray floret limb bluish violet.* It is not clear if this character occurs in all *Allardia* species. Some may have whitish rays.

Cancrinia

35 *Capitula discoid.*

Cancriniella

35 *Capitula discoid.*

39 *Involucral bracts in 1–2 rows, rather wide.* According to Tzvelev (in Komarov, 1961) this character distinguishes *Cancriniella* from *Cancrinia*.

48 *Receptacle pilose.*

161 *Pappus of short (not large and obovate or bristle-like) scales, an auricle, a corona, or absent.*

9. **TRICHANTHEMIS** Regel & Schmalh. in *Trudy imp. S.-Peterb. bot. Sada* **5:** 617 (1877). Type species: *T. karataviensis* Regel & Schmalh. – *Glossanthis* Polj.

Basally much woody half-shrubs with erect annual stems basally covered in sheathing leaf bases. Leaves alternate and basally rosulate, pinnatisect. Capitula solitary, pedunculate, radiate or discoid. Involucral bracts with or without dark brown margins. Receptacle convex, generally densely hirsute, epaleate. Ray florets female, fertile; limb white, pale pink, or yellow, many-veined; tube generally pilose. Disc corolla 5-lobed, generally pilose; hairs subulate, with a few basal cells and one long apical cell. Cypselas 7–10-ribbed, densely pilose with the same type of hairs as on the florets, sometimes with myxogenic cells. Pappus of 4–12 large, white, linear to oblong scales at least half as long as the corolla.

DISTRIBUTION. C. Asia. – 9 spp.

Trichanthemis has several unusual features such as the hirsute receptacle and the pilose corollas and cypselas. The relationship to *Cancrinia* and its relatives was noted by Poljakov (1959), who placed several of the present discoid *Trichanthemis* species in *Cancrinia*. He also defined *Trichanthemis* as discoid and removed the radiate species to a new genus *Glossanthis*. His treatment has not been followed by later authors, e.g. Tzvelev in *Flora URSS* (Komarov, 1961). Tzvelev noted that the radiate *T. aurea* and *T. radiata* are related to the discoid *T. paradoxos* and *T. karataviensis*, respectively. He also indicated the possible relationship between the problematic *Xylanthemum tianshanicum* (*Pyrethrum tianshanicum*) and *Trichanthemis*, notably *T. butkovii*. Another intergeneric relationship in need of investigation is that of *Ugamia* and *Trichanthemis*. Some discoid, small-leaved species of *Trichanthemis* may be more closely related to *Ugamia* than to other *Trichanthemis* species. It appears that *Trichanthemis* may be paraphyletic. Small segregates, possibly *Ugamia* for example, or even larger ones in *Tanacetum* may have their sister groups within *Trichanthemis*.

The list of species is taken from *Flora URSS* and *Flora iranica* but with one former synonym re-established as a species (*T. simulans*; Pavlov, 1966).

T. afghanica Podl.
T. aulieatensis (B. Fedtsch.) H. Kraschen.
**T. aurea* H. Kraschen.
**T. butkovii* Kovalevsk.
T. karataviensis Regel & Schmalh.
**T. litwinowii* (H. Kraschen) Tzvelev
T. paradoxos (Winkler) Tzvelev
T. radiata H. Kraschen. & Vved.
**T. simulans* (Pavlov) Pavlov

10. **UGAMIA** Pavlov in *Vest. Akad. Nauk Kazakh. SSR* **8**:25 (1950). Type species: *U. trichanthemoides* Pavlov (*U. angrenica* (H. Kraschen.) Tzvelev).

A compact, tomentose, basally much woody half-shrub. Leaves alternate to rosulate, densely set, small, pectinate. Capitula solitary on short, nodding peduncles, discoid. Involucral bracts with dark brown margins. Receptacle almost flat, epaleate. Corolla 5-lobed. Cypselas 10–15-ribbed, densely pilose; hairs subulate, with a few basal cells and one long apical cell. Pappus of 10–15 white linear scales roughly as long as the corolla.

DISTRIBUTION. C. Asia. – Monotypic.

Ugamia angrenica is very characteristic with its compact and woody habit, small, pectinate leaves and campanulate capitula on short, nodding peduncles. Though discoid as in *Cancrinia* and *Cancriniella*, it is possibly most closely related to part of *Trichanthemis*, which also has discoid representatives, with densely pilose cypselas.

11. **RICHTERIA** Karelin & Kir. in *Bull. Soc. Nat. Moscou* **15**:126 (1842). Type species: *R. pyrethroides* Karelin & Kir.

Tomentose half-shrubs, basally woody with stems covered in sheathing leaf bases. Leaves alternate and basally rosulate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucral bracts with dark brown margins. Receptacle convex, epaleate. Ray florets female; limb white. Disc corolla 5-lobed. Cypselas faintly 6–10-ribbed, with sessile glands. Pappus of 6–10 obovate, apically brownish scales at least half as long as the corolla.

DISTRIBUTION. Iran, Afghanistan, C. Asia, Mongolia, China in Xinjiang and Tibet, Himalaya. – 3 spp.

Richteria is commonly treated as part of *Pyrethrum* (i.e. *Tanacetum* s.l.), but since it was originally described as a genus we find it suitable to retain it as such and improve the circumscription of *Tanacetum* (incl. *Pyrethrum*) by restricting it to those species with a short coroniform or auriculate pappus.

Richteria approaches *Trichanthemis* in habit; the somewhat pedunculoid stems are basally covered in more or less sheathing leaf bases and the leaves are mainly basally arranged. This appears to be a plesiomorphic condition within the tribe, since a similar habit is shown by representatives of the outgroup. The pappus scales are apically brownish as in *Cancrinia* and *Allardia*, though in the latter genus they are more narrow and numerous. Being white-rayed rather than discoid or blue-rayed, *Richteria* is plesiomorphic and appears undefined compared to the latter two genera.

Two species of *Richteria* have been described and one more is added here but there may be more species hidden within *Tanacetum*.

R. djilgense (Franchet) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum djilgense* Franchet in *Bull. Mus. Hist. nat. Paris* **2**:345 (1896) (*Pyrethrum djilgense* (Franchet) Tzvelev, *Tanacetum djilgense* (Franchet) Podl.).

R. leontopodium Winkler

R. pyrethroides Karelin & Kir. (*Pyrethrum arassanicum* (Winkler) O. & B. Fedtsch., *Pyrethrum neglectum* Tzvelev, *Pyrethrum pyrethroides* (Karelin & Kir.) B. Fedtsch. & H. Kraschen., *Pyrethrum transiliense* (Herder) Regel & Schmalh., *Tanacetum pyrethroides* (Karelin & Kir.) Schultz-Bip.) – *Note:* Synonymy after Kovalevskaja (in Vvedensky, 1962: 133) and Podlech (in Podlech et al., 1986).

12. **ALLARDIA** Decne in Jacquemont, *Voy. Inde* **4**: 87 (1842–7). Type species: *A. tomentosa* Decne. – *Waldheimia* Karelin & Kir.

Glabrous to densely tomentose perennial herbs. Leaves alternate to rosulate, densely set, pinnatifid. Capitula solitary, pedunculate, radiate. Involucral bracts with dark brown margins. Receptacle convex, epaleate. Ray florets female, fertile or sterile, or neuter; limb white, pink, or bluish-violet. Disc corolla 5-lobed, with a yellow or bluish-violet limb. Cypselas faintly 5–10-ribbed, generally with sessile glands, sometimes pilose. Pappus of many bristle-like, subulate, apically brownish scales as long as or longer than the corolla.

DISTRIBUTION. Afghanistan, C. Asia, Mongolia, China in Sinkiang and Tibet, and Himalaya. – 8 spp.

With its white to pink and blue-violet florets and cypselas with pappus bristles *Allardia* may seem out of place in the Anthemideae but it is clearly a member of this tribe. The pappus 'bristles' are subulate, much elongated scales, similar to those of *Ugamia* (in shape and number) and *Richteria* and *Cancrinia* (in being apically brownish). Several narrow bristles are probably plesiomorphic, and apically brownish bristles are probable synapomorphies for *Allardia* and the latter two genera. Tzvelev in *Flora URSS* (Komarov, 1961) also stated that the genus is related to *Richteria*.

The publication dates of the various parts of Jacquemont's *Voyage dans l'Inde* are still in dispute, but it appears that pp. 1–88 of volume 4 were published before 1842 (Stafleu & Cowan, 1979). *Allardia* is then prior to *Waldheimia*, which was published in 1842. *Allardia* was typified by Tzvelev in *Flora URSS* (Komarov, 1961). He used *Waldheimia* for the section name and *Waldheimia tomentosa* (*Allardia tomentosa*) as the type species.

**A. huegelii* Schultz-Bip. (*Waldheimia huegelii* (Schultz-Bip.) Tzvelev)

A. lasiocarpa (G. X. Fu) Bremer & Humphries, **comb. nov.** Basionym: *Waldheimia lasiocarpa* G. X. Fu in Shih & Fu, *Acta phytotax. sin.* **17:** 113 (1979).

A. nivea Hook. f. & Thomson ex C. B. Clarke (*Waldheimia nivea* (C. B. Clarke) Regel)

**A. stoliczkae* C. B. Clarke (*Waldheimia stoliczkae* (C. B. Clarke) Ostenf.)

A. tomentosa Decne (*Waldheimia tomentosa* (Decne) Regel, *Tanacetum tomentosum* (Decne) Muradyan)

A. transalaica (Tzvelev) Bremer & Humphries, **comb. nov.** Basionym: *Waldheimia transalaica* Tzvelev in Komarov, *Fl. URSS* **26:** 875 (1961).

A. tridactylites (Karelin & Kir.) Schultz-Bip. (*A. glabra* Decne, *Tanacetum glabrum* (Decne) Muradyan, *Waldheimia glabra* (Decne) Regel, *Waldheimia tridactylites* Karelin & Kir.), *Note: A. glabra* was reduced by Kovalevskaja (in Vvedensky, 1962:188).

A. vestita Hook. f. & Thomson ex C. B. Clarke (*Waldheimia vestita* (C. B. Clarke) Pampan.)

13. **CANCRINIA** Karelin & Kir. in *Bull. Soc. Nat. Moscou* **15:** 124 (1842). Type species: *C. chrysocephala* Karelin & Kir.

Compact tomentose perennial herbs. Leaves alternate to rosulate, densely set, pinnatifid. Capitula solitary, pedunculate, discoid. Involucral bracts with dark brown margins. Receptacle convex, epaleate. Corolla 5-lobed with a narrow tube and a distinct limb. Cypselas faintly 7–9-ribbed, glabrous or sparsely pilose. Pappus of 5–12 lanceolate, apically brownish scales as long as or slightly longer than the corolla.

DISTRIBUTION. C. Asia, Mongolia and China in Xinjiang. – 4 spp.

Cancrinia, originally described as monotypic, was expanded to include some 20 species, mainly from *Tanacetum*, by Poljakov (1959) and Tzvelev in *Flora URSS* (Komarov, 1961). Tzvelev divided the genus into four sections. Most of the species do not belong together with the type species, *C. chrysocephala* and its sister species, *C. tianshanica*. Tzvelev's sect. *Polychrysum* and sect. *Tanacetopsis* were elevated to genera by Kovalevskaja (in Vvedensky, 1962). The monotypic section *Matricarioides* (*C. discoidea*) is transferred to *Matricaria*. *Cancrinia* and *Allardia* are possibly more closely related than indicated by the cladogram. They are similar in habit and cypsela morphology, though *Allardia* has more and narrower pappus scales.

C. chrysocephala Karelin & Kir.
**C. krasnoborovii* V. Khan.
C. pamiralaica (Kovalevsk.) Kovalevsk.
**C. tianshanica* (H. Kraschen.) Tzvelev

14. **CANCRINIELLA** Tzvelev in Komarov, *Fl. URSS* **26:**876 (1961). Type species: *C. krascheninnikovii* (Rubtzov) Tzvelev.

A compact, hirsute, basally woody half-shrub. Leaves alternate to rosulate, densely set, pectinate. Capitula solitary, long-pedunculate, discoid. Involucral bracts in 1–2 rows, rather wide, subequal. Receptacle convex, sparsely pilose, epaleate. Corolla 5-lobed. Cypselas 10-ribbed. Pappus a corona of scales.

DISTRIBUTION. C. Asia. – Monotypic.

This monotypic genus is supposed to be related to *Cancrinia*. Poljakov (1959) stated that it is related to *Trichanthemis karataviensis*, and he placed both species in *Cancrinia*.

3. 'TANACETINAE' Bremer & Humphries, **subtrib. nov.**

Type species: *Tanacetum vulgare* L.

Herbae perennes vel frutices vel raro herbae annuae. Cypselae plerumque oblongae et plus quam quinquecostatae. Pappus coroniformis e squamis distinctis vel auricula adaxiali formatus, vel nullus.

Perennial herbs or shrubs, rarely annuals. Leaves alternate or sometimes rosulate, generally pinnatisect, rarely entire or few-lobed. Capitula solitary or corymbose, generally pedunculate, radiate, disciform or discoid. Involucral bracts sometimes with dark brown margins. Receptacle flat to conical, epaleate or rarely paleate (*Heliocauta*). Ray floret limb white, yellow or pink. Disc corolla 5-lobed. Cypselas often oblong and more than 5-ribbed, rarely dorsiventrally flattened (*Heliocauta*), sometimes with sessile glands and myxogenic cells. Pappus a corona, or of separate scales, or an adaxial auricle, or absent.

DISTRIBUTION (Table 9). C. Asia but also in N. America and N. Africa, some *Tanacetum* species introduced in the S. hemisphere. – 7 genera, 213 spp.

The genera of this subtribe, 'Tanacetinae', have no synapomorphies in common. The subtribe is probably paraphyletic (see for example, Schultz Bipontinus, 1844*a*), and hence put within inverted commas following the convention suggested by Patterson & Rosen (1977) and Wiley (1981). There is still a lot of work to be undertaken on the classification of Anthemideae, and *Tanacetum* particularly is a key genus of the tribe. At the present state of knowledge we have felt it necessary to adopt a provisional subtribe comprising *Tanacetum* and a number of odd genera apparently related to this genus.

There are several segregate genera and groups of genera, possibly even whole subtribes, which are related to parts of *Tanacetum*, which is thus paraphyletic as presently circumscribed. Apparent examples of such genera are those classified in this subtribe. Subtribes which probably have their sister groups within *Tanacetum* include Gonosperminae, Handeliinae, and Artemisiinae. The remaining subtribes, excluding Ursiniinae and Cancriniinae, may form one group (as indicated by the cladogram) or a number of groups also with their sister groups within *Tanacetum*. In fact, *Tanacetum* is a paraphyletic group basal to large parts of the tribe. The cladogram shown here is the single most parsimonious one derivable from the present data matrix, but the picture may be quite different when *Tanacetum* is resolved into smaller monophyletic units. The whole complex is in need of detailed investigation, both on the generic and the specific level.

Clades and characters – Fig. 4, Tables 2, 10.

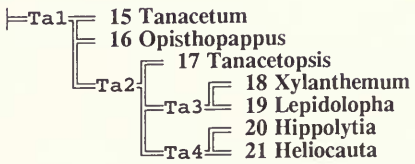

Fig. 4 Cladogram of the 'Tanacetinae' produced by the *ie* option in Hennig86. Cladogram length = 16, consistency index = 100, retention index = 100.

Provisional group Ta1 – subtribe 'Tanacetinae'

There is no autapomorphy for this group, but as explained above *Tanacetum* probably contains the sister groups of the other genera.

Tanacetum

175 *Embryo sac tetrasporic.* The 10 *Tanacetum* species investigated embryologically (Harling 1951; see discussion under *Tanacetum*) are all tetrasporic. The other genera of 'Tanacetinae' have not been investigated.

Opisthopappus

163 *Pappus of separate, mainly abaxial, subulate scales.*

Table 9 General distribution of Tanacetinae and genera. x=indigenous, o=introduced.

	N.Am.	Eur-Asia	C.& E. Asia	SW Asia	S.Eur.	N.Afr.	S.Afr.	Austr. N.Zeal.	S.Am.
Tanacetinae	x	x	x	x	x	x	o	o	o
Tanacetum	x	x	x	x	x	x	o	o	o
Opisthopappus			x						
Tanacetopsis			x						
Xylanthemum		x	x						
Lepidolopha			x						
Hippolytia			x	x					
Heliocauta						x			

Table 10 Data matrix for the Tanacetinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1 5	4 3	5 2	0 7	1 a	5 1	7 8	6 1	1 5	7 3	6 5	3 2	3 6	4 7	5 8	7 4	2 1	9 2	4 5	0 2	1 5	3 0	4 4	8 1	7 6	5 0	1 3	5 3	5 3	5 5	6 6	7 7	9 9	0 0	6 7	1 5	7 1	6 5	6 6	6 8	7 0	2 4	1 4	6 6	1 8	8 9	1 1	9 1	1 6	2 2
15. *Tanacetum*	a	1	a	a	1	1	1	1	0	p	0	p	0	0	p	0	0	p	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	p	p	p	p	p	p	p	p	p
16. *Opisthopappus*	a	1	a	a	1	?	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17. *Tanacetopsis*	a	1	?	a	1	?	1	?	0	1	0	0	0	0	p	0	0	p	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0
18. *Xylanthemum*	a	1	a	a	1	?	1	?	0	a	1	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19. *Lepidolopha*	a	1	?	a	1	?	1	?	0	1	1	0	1	1	0	0	0	p	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	p	0	0	0	0	0	0	0
20. *Hippolytia*	a	1	?	a	1	?	1	?	0	1	0	?	0	0	a	a	1	a	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	p	0	0	0	0	0	0	0
21. *Heliocauta*	a	1	?	a	1	?	1	?	0	1	0	?	0	0	a	a	1	0	0	a	1	1	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0

Clade Ta2

35 *Capitula discoid.* For reasons of parsimony the five genera of this clade are grouped together, though they probably have different sister groups within *Tanacetum*. The radiate species *Xylanthemum tianshanicum* is probably misplaced in this genus.

Tanacetopsis

There is no autapomorphy for this genus.

Clade Ta3

2 *Plants shrubby.*

Xylanthemum

166 *Pappus adaxially long.*

Lepidolopha

37 *Involucre rather narrowly urceolate.*

38 *Involucral bracts in 4–7 rows.*

Clade Ta4

44 *Involucral bracts with dark brown margins.* This character is present also in several *Tanacetum* and some *Tanacetopsis* species.

51 *Floral parts with resin canals.* Floral resin canals also occur in scattered species of the other genera of the subtribe.

172 *Pappus absent in ray and disc cypselas.*

Hippolytia

29 *Capitula densely corymbose.* Corymbose capitula are common in *Tanacetum* and present also in some species of *Tanacetopsis* and *Lepidolopha*. Some specialized alpine species of *Hippolytia* have solitary capitula.

92 *Anthers caudate.*

Heliocauta

45 *Receptacle paleate.*

100 *Style immersed in a lobed nectary.*

114 *Cypselas dorsiventrally flattened.*

138 *Cypselas with scattered elongated resin sacs.*

15. **TANACETUM** L., *Sp. pl.*: 1028 (1753). Type species: *T. vulgare* L. – *Balsamita* Miller – *Gymnocline* Cass. – *Hemipappus* K. Koch – *Pyrethrum* Zinn – *Spathipappus* Tzvelev.

Perennial, rarely annual herbs or seldom small, basally woody half-shrubs. Leaves alternate or rarely rosulate, pinnatifid to pinnatisect or rarely entire, serrate. Capitula solitary or corymbose, radiate, disciform, or discoid. Involucral bracts sometimes with a dark brown margin. Receptacle flat or convex, epaleate. Ray florets female or neuter; limb yellow, white, or pink. Disc corolla 5-lobed. Cypselas generally oblong, 5–12-ribbed, often with sessile glands, never with myxogenic cells. Pappus a short or well developed corona, sometimes of short free scales, rarely an adaxial auricle (very rarely absent). Embryo sac tetrasporic.

DISTRIBUTION. Europe and temperate Asia, also in N. Africa (*T. annuum*, *T. corymbosum*) and several species in N. America, some species introduced in the S. hemisphere. – 152 spp.

Tanacetum s. l. is a large and poorly understood boreal genus with many little-known Asian representatives. Variation in habit, foliage, inflorescences, and capitula structure is considerable. As presently circumscribed, the genus may be recognized by the epaleate receptacle and the non-myxogenic, generally straight and ribbed cypselas with a coroniform or rarely auriculate pappus. Occasional species with epappose cypselas currently placed in *Tanacetum* are probably mis-

placed and are likely to be transferred to other genera.

One example of a probable misplaced species is *T. microphyllum*, with triangular apical anther appendages and thin-walled, obovoid cypselas with minute pappus scales and no ribs. These characters are reminiscent of subtribe Artemisiinae, where this species probably should be accommodated.

Pyrethrum differs from *Tanacetum* s. s. by its white or pink rays. *Tanacetum* s. s. has discoid or disciform capitula or, if radiate, with yellow rays. Tzvelev (in Komarov, 1961) diagnosed *Pyrethrum* as white-rayed and *Tanacetum* as yellow-rayed or disciform (heterogamous). He classified discoid (homogamous) species in *Cancrinia*. Tzvelev also noted the heterogeneous nature of *Pyrethrum* and speculated that *Cancrinia* (s. l.) evolved from *Pyrethrum* by loss of rays, whereafter *Tanacetum* (s. s.) evolved from *Cancrinia* by transformation of the outer, yellow disc florets into short, yellow rays. Except for the often short lamina the yellow rays of *Tanacetum* (s. s.) are similar to the white or pink ones of *Pyrethrum*. In other Anthemideae, e.g. *Cotula*, where pseudorays have evolved from the disc florets, their discoid nature is clearly recognized. Also ray colour is very homoplasious within the tribe, many well-defined genera having species with both white and yellow rays. The relationship between *Pyrethrum* and *Tanacetum* s. s. is close and involves several sister group relationships between species and groups of species currently classified in the two genera. We follow Heywood in *Flora europaea* (Tutin et al., 1976; also Heywood, 1954) and Grierson in *Flora of Turkey* (Davis, 1975) in uniting the two genera.

Tzvelev (in Komarov, 1961) recognized 14 sections of *Pyrethrum* and four sections of *Tanacetum*. Sections *Leucanthemopsis* and *Pyrethrum* section *Richteria* are considered by us as separate genera in different subtribes. Section *Balsamita* (*T. balsamita*) is sometimes considered as a separate genus distinguished by its entire, serrate leaves. Harling (1951) in describing the unusual tetrasporic embryo sac development and Favarger (1966) referring to chemistry both recommended that *Balsamita* should be kept separate from *Tanacetum*. The actual presence of a tetrasporic embryo sac in *Balsamita* seems to strengthen its position within *Tanacetum* (together with the type species *T. vulgare* and others), though there is a difference in embryo sac development. Chemical evidence is far too scattered to support a removal of *Balsamita* from *Tanacetum*. In morphology *Balsamita* is similar to several representatives of *Pyrethrum* sensu Tzvelev and we follow him and Grierson in *Flora of Turkey* (Davis, 1975) in reducing *Balsamita* to synonymy.

Tzvelev's other sections of *Pyrethrum* and *Tanacetum* are a mixture of isolated and, in most cases, vaguely defined entities. *Pyrethrum* sect. *Trichanthemopsis* with the single species *P. tianshanicum* has been transferred to *Xylanthemum*. Other more or less isolated sections are the woody *Pyrethrum* sect. *Xylopyrethrum* and *Tanacetum* sect. *Asterotricha*. The woody sections, subtribe Cancriniinae, and the shrubby genera *Xylanthemum* and possibly also *Lepidolopha* may be more closely related than indicated by the present classification.

Harling (1951) reported tetrasporic embryo sacs in all 10 species of *Tanacetum* so far investigated (*T. balsamita*, *T. camphoratum*, *T. cinerariifolium*, *T. coccineum* (*Chrysanthemum marschallii*), *Tanacetum corymbosum*, *T. macrophyllum*, *T. millefolium*, *T. parthenium*, *T. roseum* and *T. vulgare*. Interestingly, these species represent nine of Tzvelev's different sections, but not the more isolated ones mentioned above.

Tzvelev accepted only heterogamous (disciform or yellow-rayed) species in *Tanacetum* s. s. Thus the discoid *T. argenteum* was accommodated in the genus *Hemipappus*, further distinguished by its auriculate pappus. On other characters *Hemipappus* fits well into *Tanacetum* and it was not accepted as a genus by Grierson in *Flora of Turkey*, who included not only *T. argenteum* but also some related Turkish endemic species (*T. depauperatum*, *T. haradjanii*, *T. tomentellum*) in *Tanacetum*. This solution is followed here, and we include other species with an auriculate pappus in *Tanacetum* (formerly *Spathipappus*, discussed below). Except for the pappus there are no indications that *Hemipappus* and *Spathipappus* are closely related sister groups.

Spathipappus described by Tzvelev in *Flora URSS*, is supposed to differ from *Pyrethrum* by its auriculate pappus and sterile rays. Muradyan (1970) found that the fruits are very similar to those of other *Tanacetum* species and transferred *S. griffithii* to *Tanacetum*. The other two species, *S. chitralensis* and *S. porphyrostephanus*, are recombined here.

The list of species is compiled mainly from *Flora europaea* (Tutin et al., 1976), *Flora of Turkey* (Davis, 1975), and *Flora URSS* (Komarov, 1961, including *Pyrethrum*) with species described later or from other areas added.

T. abrotanifolium (L.) Druce. Turkey, Caucasus, Iran.

T. abrotanoides Bremer & Humphries, **nom. nov**. Basionym: *Pyrethrum abrotanifolium* Bunge ex Ledeb., *Fl. ross.* **2:** 549 (1845) – *Note:* In *Tanacetum* the epithet *abrotanifolium* is already occupied by the preceding species in the list. C. Asia, China in Xinjiang.

T. achilleifolium (M. Bieb.) Schultz-Bip. E. Europe, C. Asia.

T. akinfievii (Alexej.) Tzvelev. Caucasus.

T. alatavicum Herder (*Pyrethrum alatavicum* (Herder) O. & B. Fedtsch.). C. Asia, Mongolia, China in Xinjiang.

T. albipannosum Huber-Mor. & Grierson. Turkey.

T. alyssifolium (Bornm.) Grierson. Turkey.

T. annuum L. SW Europe in France, Spain, and Portugal, N. Africa in Morocco.

***T. arctodzhungaricum** (Golosk.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum arctodzhungaricum* Golosk. in *Bot. Mater. Gerb. Inst. Bot. Akad. Nauk Kazakh. SSR* **7:** 35 (1971). C. Asia.

T. archibaldii Podl. Iran.

T. argenteum (Lam.) Willd. (*Hemipappus argenteus* (Lam.) Tzvelev, *Hemipappus canus* K. Koch). Turkey, Middle East, Caucasus.

**T. argyranthemoides* (Boiss. & Kotschy) Schultz-Bip. Iran.

T. armenum (DC.) Schultz-Bip. (*Pyrethrum heldreichianum* Fenzl ex Tchich.). Turkey.

T. aromaticum (Tzvelev) Bremer & Humphries, **comb. nov**. – Basionym: *Pyrethrum aromaticum* Tzvelev in Komarov, *Fl. URSS* **26**: 222 (1961). – *Note:* the name *Pyrethrum aromaticum* must be considered a new species described by Tzvelev, and not a new combination based on *Tripleurospermum aromaticum* Rupr. ex Boiss. as stated by Tzvelev. That name was only published pro syn. by Boissier (1875: 334). Caucasus.

**T. artemisioides* Schultz-Bip. in Hook. f. Himalaya.

**T. atkinsonii* (C. B. Clarke) Kitam. (*Pyrethrum atkinsonii* (C. B. Clarke) Ling & Shih). China, Himalaya.

T. aucheranum (DC.) Schultz-Bip.(*Pyrethrum aucheranum* DC.). Turkey, Caucasus.

T. aucheri DC. Turkey, Syria, Lebanon, Israel.
T. audibertii (Req.) DC. Sardinia.
T. balsamita L. (*Balsamita major* Desf., *Pyrethrum balsamita* (L.) Willd., *Pyrethrum balsamitoides* (Náb.) Tzvelev, *Pyrethrum majus* (Desf.) Tzvelev). SW Asia from Turkey, Caucasus, Iran, and Afghanistan, also widely cultivated and naturalized.
T. bamianicum Podl. Afghanistan.
**T. barclayanum* DC. (*T. turlanicum* (Pavlov) Tzvelev). C. Asia, China in Xinjiang.
T. bipinnatum (L.) Schultz-Bip. NE Europe, Siberia, Alaska.
T. boreale Fischer ex DC. Siberia, C. Asia and Far East, China, Korea, Alaska, Canada.
T. budjurnense (Rech. f.) Tzvelev. Iran.
**T. cadmeum* (Boiss.) Heyw. Turkey.
T. camphoratum Less. Western N. America from British Columbia S. to California.
T. canescens DC. (*T. gilliatii* (Turrill) Parsa, *T. modestum* (Heimerl ex Stapf) Parsa). Turkey, Caucasus, Iran.
T. cappadocicum (DC.) Schultz-Bip. Turkey.
T. changaicum (H. Kraschen. ex Grubov) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum changaicum* H. Kraschen. ex Grubov in *Bot. Mater. Gerb. bot. Inst. V. A. Komorova* **27**: 23 (1955). Mongolia.
T. chiliophyllum (Fischer & C. Meyer) Schultz-Bip. (*T. heimerli* (Náb.) Parsa, *T. oligocephalum* (DC.) Schultz-Bip.). Turkey, Caucasus, Iraq, Iran.
T. chitralense (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Spathipappus chitralensis* Podl., *Fl. iranica* **158:** 151 (1986). Pakistan.
T. cilicium (Boiss.) Grierson. Turkey, Middle East, Iraq.
T. cinerariifolium (Trevir.) Schultz-Bip. (*Pyrethrum cinerariifolium* Trevir). SE and E. Europe, Caucasus, C. Asia, China, often cultivated as the source of the insecticide pyrethrin.
T. coccineum (Willd.) Grierson (*Pyrethrum coccineum* (Willd.) Vorosch., *Pyrethrum chamaemelifolium* (Sommier & Levier) Sosn.). Turkey, Caucasus, Iran, often cultivated as the garden '*Pyrethrum*'.
T. corymbiforme (Tzvelev) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum corymbiforme* Tzvelev in Komarov, *Fl. URSS* **26:** 873 (1961). C. Asia, China in Xinjiang.
T. corymbosum (L.) Schultz-Bip. (*Pyrethrum corymbosum* (L.) Willd., *Pyrethrum clusii* Fischer ex Reichb.). N. Africa in Morocco and Algeria, most of Europe except N. parts, Turkey, Caucasus, C. Asia.
**T. crassipes* (Stchegl.) Tzvelev. C. Asia, China in Xinjiang.
T. daghestanicum (Rupr. ex Boiss.) Bremer & Humphries, **comb. nov**. Basionym: *Chamaemelum daghestanicum* Rupr. ex Boiss., *Fl. orient.* **3**: 334 (1875) (*Pyrethrum daghestanicum* (Rupr. ex Boiss.) Rupr. ex Flerov). Caucasus.
***T. demetrii** (Manden.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum demetrii* Manden. in *Zametki Sist. Geogr. Rast.* **22:** 60 (1961). Caucasus.
T. densum (Labill.) Schultz-Bip. Turkey.
T. depauperatum (Post) Grierson. Turkey.
T. dolomiticum (Galushko) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum dolomiticum* Galushko in *Novit. Syst. Pl. Vasc. Acad. Sci. URSS* **6:** 218 (1970). Caucasus.
**T. dumosum* Boiss. Iran.
T. eginense (Hausskn. ex Bornm.) Grierson. Turkey.
**T. elongatum* (Bornm. & Gauba) Parsa. Iran.
**T. falcatolobatum* H. Kraschen. (*Cancrinia maximoviczii* Winkler). China.
T. falconeri Hook. f. Himalaya.
T. ferulaceum (Webb ex Berth.) Schultz-Bip. Canary Islands.
**T. funkii* Schultz-Bip. ex Willk. SW Europe in Spain.
**T. galae* (Popov) Nevski (*Pyrethrum galae* Popov). C. Asia.
T. galushkoi (Prima) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum galushkoi* Prima in *Nov. Sist. Vysshikh Rast.* **11:** 277 (1974). Caucasus.
T. germanicopolitanum (Bornm. & Heimerl) Grierson. Turkey.
T. ghoratense Podl. Afghanistan.
T. glanduliferum (Sommier & Levier) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum glanduliferum* Sommier & Levier, *Decas Comp. Nov. Cauc.* **87** (1895). Caucasus.
**T. griffithii* (C. B. Clarke) Muradyan (*Spathipappus griffithii* (C. B. Clarke) Tzvelev). Afghanistan, C. Asia, Himalaya.
T. grossheimii (Sosn.) Muradyan (*Pyrethrum grossheimii* Sosn.). Caucasus, Iran.
T. haradjanii (Rech. f.) Grierson. Turkey.
**T. haussknechtii* (Bornm.) Grierson. Turkey.
**T. herderi* Regel & Schmal. SW Asia.
**T. heterotomum* (Bornm.) Grierson. Turkey.
T. hissaricum (H. Kraschen.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum hissaricum* H. Kraschen. in *Feddes Reprium* **26:** 26 (1929). C. Asia.
T. hololeucum (Bornm.) Podl. Iran.
T. huronense Nutt. N. America in Alaska, Canada and Michigan.
T. karelinianum Bremer & Humphries, **nom. nov**. Basionym: *Pyrethrum karelinii* H. Kraschen. in *Nov. Sist. Vysshikh Rast.* **9:** 157 (1946). C. Asia.
**T. karelinii* Tzvelev. C. Asia.
T. kaschgarianum Bremer & Humphries, **nom. nov**. Basionym: *Pyrethrum kaschgaricum* H. Kraschen. in *Nov. Sist. Vysshikh Rast.* **9:** 158 (1946) (non *T. kaschgaricum* H. Kraschen.). China.
T. kelleri (Krylov & Plotn.) Takht. (*Chrysanthemum kelleri* Krylov & Plotn., *Pyrethrum kelleri* (Krylov & Plotn.) H. Kraschen.). C. Asia.
T. khorassanicum (H. Kraschen.) Parsa (*T. czerniakowskae* (H. Kraschen.) Parsa). Iran.
T. kotschyi (Boiss.) Grierson (*Pyrethrum kotschyi* Boiss.). Turkey, Caucasus, Iraq, Iran.
T. krylovianum (H. Kraschen.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum krylovianum* H. Kraschen. in *Bot. Mater. Gerb. bot. Inst. V. A. Komorova* **9:** 155 (1946). C. Asia, China in Xinjiang.
**T. kubense* (Grossh.) Muradyan (*Pyrethrum kubense* Grossh.). Caucasus.
**T. lanuginosum* Schultz-Bip. & Herder (*Pyrethrum lanuginosum* (Schultz-Bip. & Herder) Tzvelev). E. Siberia, Mongolia.
T. leptophyllum (Steven) Schultz-Bip. (*Pyrethrum leptophyllum* Steven). Caucasus.
**T. longipedunculatum* (Sosn.) Tzvelev. Caucasus.
**T. macrocephalum* Pampan. Himalaya.
T. macrophyllum (Waldst. & Kit.) Schultz-Bip. (*Pyrethrum macrophyllum* (Waldst. & Kit.) Willd.). C. and SE Europe, Turkey, Caucasus.
T. marionii (Albov) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum marionii* Albov in *Bull. Herb. Boissier* **3:** 92 (1895). Caucasus.

T. maymanense Podl. Afganistan.
T. microphyllum DC. SW Europe in Spain and Portugal.
**T. mikeschinii* (Tzvelev) Takht. (*Pyrethrum mikeschinii* Tzvelev). C. Asia.
T. millefolium (L.) Tzvelev (*T. kittaryanum* (C. Meyer) Tzvelev). E. Europe, S. Siberia, C. Asia.
**T. mucroniferum* Huber-Mor. & Grierson. Turkey.
T. mucronulatum (Hoffsgg & Link) Heyw. SW Europe in Portugal.
T. nitens (Boiss. & Noë) Grierson. Turkey.
T. nivale Schultz-Bip. Iraq.
T. niveum (Lagasca) Schultz-Bip. (*Pyrethrum fruticulosum* Biehler). Caucasus.
T. nuristanicum Podl. Afghanistan.
**T. odessanum* (Klokov) Tzvelev. E. Europe.
T. oltense (Sosn.) Grierson. Turkey.
T. ordubadense (Manden.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum ordubadense* Manden. in *Nov. Sist. Vysshikh Rast.* **19**: 358 (1959). Caucasus.
T. oxylepis (Bordz.) Grierson. Caucasus, Turkey.
T. oxystegium (Sosn.) Grierson. Turkey.
**T. paczoskii* (Zef.) Tzvelev. Krym.
T. pakistanicum Podl. Pakistan.
T. paleaceum Podl. Afghanistan.
**T. paradoxum* Bornm. Iran.
T. parthenifolium (Willd.) Schultz-Bip. (*Pyrethrum parthenifolium* Willd.). SW Asia from Turkey to Caucasus, Iran, Aghanistan, and C Asia.
T. parthenium (L.) Schultz-Bip. (*Pyrethrum parthenium* (L.) Smith). N. Africa, SE and E. Europe, SW Asia from Turkey to Caucasus, Iran, Aghanistan, and C. Asia, also widely naturalized.
**T. petiolosum* Pampan. Himalaya.
T. petrareum (Shih) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum petrareum* Shih in *Bull. bot. Lab. n.-east For. Inst.* **6:** 10 (1980). China.
***T. peucedanifolium** (Sosn.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum parthenifolium* Willd. var. *peucedanifolium* Sosn. in *Trudy tiflis. bot. Sada* **17:** 35 (1915) (*Pyrethrum peucedanifolium* (Sosn.) Manden.). Caucasus.
**T. pinnatum* Boiss. (*T. flavovirens* (Boiss.) Tzvelev, *T. tamrutense* (Sosn.) Sosn.). Turkey, Caucasus, Iraq, Iran.
T. podlechii Bremer & Humphries, **nom. nov**. Basionym: *Pyrethrum komarovii* Sosn. in *Dokl. Akad. Nauk armyan. SSR* **2** (4): 119 (1945) (non *Tanacetum komarovii* (Winkler) Muradyan). Caucasus.
T. polycephalum Schultz-Bip. (*T. argyrophyllum* (K. Koch) Tzvelev, *T. duderanum* (Boiss.) Tzvelev, *T. heterophyllum* Boiss., *T. junesarense* (Bornm.) Parsa, *T. myriophyllum* Willd.). Turkey, Caucasus, Iraq, Iran.
T. porphyrostephanum (Rech. f.) Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum porphyrostephanum* Rech. f., *Symb. Afghan.* **2:** 47 (1955) (*Spathipappus porphyrostephanus* (Rech. f.) Tzvelev). Iran.
T. poteriifolium (Ledeb.) Grierson (*Pyrethrum poteriifolium* Ledeb.). Turkey, Caucasus.
T. praeteritum (Horw.) Heyw. Turkey.
T. pseudoachillea Winkler. C. Asia.
T. ptarmiciflorum (Webb & Berth.) Schultz-Bip. Canary Islands.
**T. pulchellum* (Turcz.) Schultz-Bip. (*Pyrethrum pulchellum* Turcz.). E. Siberia.
T. pulchrum (Ledeb.) Schultz-Bip. (*Pyrethrum pulchrum* Ledeb.). C. Asia, Mongolia, China in Xinjiang.
T. punctatum (Desr.) Grierson (*Pyrethrum punctatum* (Desr.) Bordz. ex Sosn.). Turkey, Caucasus.
***T. richterioides** (Winkler) Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum richterioides* Winkler in *Trudy imp. S.-Peterb. bot. Sada* **10:** 86 (1887) (*Pyrethrum richterioides* (Winkler) H. Kraschen.). China.
**T. robustum* Hook. f. & Thomson ex C. B. Clarke. Himalaya.
T. roseum (Adams) Schultz-Bip. (*Pyrethrum roseum* (Adams) M. Bieb.). Caucasus.
T. roylei (DC.) Podl. W. Himalayas.
T. salsugineum Podl. Iran.
**T. sanguineum* (Parsa) Parsa. Iran.
T. santolina Winkler. S. European USSR, S. Siberia. C. Asia, China in Xinjiang.
**T. saxicolum* (H. Kraschen.) Tzvelev. C. Asia.
T. sclerophyllum (H. Kraschen.) Tzvelev. S. European USSR.
**T. scopulorum* (H. Kraschen.) Tzvelev. C. Asia, China in Xinjiang.
T. semenovii Herder (*Pyrethrum semenovii* (Herder) Winkler ex O. & B. Fedtsch.). C. Asia.
T. sericeum (Adams) Schultz-Bip. (*Pyrethrum sericeum* (Adams) M. Bieb.). Turkey, Caucasus.
T. sevanense (Sosn.) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum sevanense* Sosn. ex Gross., *Fl. Kauk.* **4:** 137 (1934). Caucasus, Iran.
T. silaifolium (Steven) Schultz-Bip. (*Pyrethrum silaifolium* Steven). Caucasus.
T. silvicola Podl. Afghanistan.
T. sinaicum (Fresen.) Del. ex Bremer & Humphries, **comb. nov**. Basionym: *Santolina sinaica* Fresen., *Mus. senckenb.* **1:** 83 (1833) (*Pyrethrum santolinoides* DC.) – *Note:* The combination *Tanacetum sinaicum* has hitherto not been validly published; it was only published pro syn. by de Candolle (1837: 59). Middle East in Sinai.
**T. sipikorense* (Bornm.) Grierson (*Pyrethrum oxylepis* (Bordz.) Tzvelev). Turkey, Caucasus.
T. songaricum (Tzvelev) Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum songaricum* Tzvelev in Komarov, *Fl. URSS* **26**: 874 (1961). C. Asia.
T. sorbifolium (Boiss.) Grierson (*Pyrethrum sorbifolium* Boiss.). Turkey, Caucasus.
**T. stapfianum* (Rech. f.) Podl. Iran.
T. tabrisianum (Boiss.) Sosn. & Takht. Turkey, Caucasus, Iran.
T. tanacetoides (DC.) Tzvelev. C. Asia, Mongolia, China in Xinjiang.
T. tatsienense (Bureau & Franchet) Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum tatsienense* Bureau & Franchet in *J. Bot.* **5**: 72 (1891) (*Pyrethrum tatsienense* (Bureau & Franchet) Ling ex Shih). China in Tibet.
T. tenuisectum (Boiss.) Podl. Iran.
T. tenuissimum (Trautv.) Gross. Caucasus, Iran, Afghanistan.
T. tirinense Podl. Afghanistan.
T. tomentellum (Boiss.) Grierson. Turkey.
T. trichophyllum (Sosn.) Bremer & Humphries, **comb. nov**. – Basionym: *Pyrethrum trichophyllum* Sosn. in *Zametki Sist. Geogr. Rast.* **15:** 2 (1949) (non Griseb.) (*Pyrethrum tricholobum* Sosn. ex Manden.). Caucasus.
T. trifoliolatum Podl. Iran.
**T. turcomanicum* (H. Kraschen.) Tzvelev. Iran, C. Asia.
**T. ulutavicum* Tzvelev. C. Asia.

T. uniflorum (Fischer & C. Meyer ex DC.) Schultz-Bip. Turkey, Caucasus, Iran.
**T. uralense* (H. Kraschen.) Tzvelev. E. Europe, S. Siberia, C. Asia.
**T. vahlii* DC. SW Europe in Spain.
T. vulgare L. Throughout most of Europe and temperate Asia, introduced in America, Australia and New Zealand.
T. walteri (Winkler) Tzvelev. Iran, C. Asia.
**T. willkommii* Schultz-Bip. SW Europe in Spain.
**T. yabrudae* (Mout.) Charpin & Dittrich (*Pyrethrum yabrudae* Mout.). Middle East in Syria.
T. zahlbruckneri (Náb.) Grierson. Turkey.

16. **OPISTHOPAPPUS** Shih in *Acta phytotax. sin.* **17:** 110 (1979). Type species: *O. taihangensis* (Ling) Shih.

Perennial herbs with basally somewhat woody stems. Leaves alternate, pinnatisect. Capitula solitary, radiate. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white or pinkish, many-veined. Disc corolla 5-lobed, with sessile glands. Cypselas obovoid, 3–5-ribbed, thin-walled, with myxogenic cells. Pappus of separate, mainly abaxial, subulate scales.

DISTRIBUTION. NE central China. – 2 spp.

The position of this genus is unclear. It appears to be a derivative of *Tanacetum*, including *Pyrethrum*, where the type species was formerly accommodated. According to Shih it differs from *Pyrethrum* and *Spathipappus* (here included in *Tanacetum*) by its thickly ribbed cypselas and by its mainly abaxial pappus of separate scales, rather than a corona or an auricle. The cypsela ribs as such are not thick but since they are invested with large myxogenic cells, dry cypselas appear thickly ribbed. The presence of myxogenic cells is indeed a character distinguishing *Opisthopappus* from *Tanacetum*, which has non-myxogenic cypselas.

O. longilobus Shih
O. taihangensis (Ling) Shih

17. **TANACETOPSIS** (Tzvelev) Kovalevsk. in Vvedensky, *Fl. uzbekistana* **6:** 138 (1962). Type species: *T. mucronata* (Regel & Schmalh.) Kovalevsk. – *Cancrinia* sect. *Tanacetopsis* Tzvelev.

Perennial herbs or basally woody half-shrubs. Leaves alternate, pinnatisect. Capitula solitary or generally laxly to densely corymbose, discoid. Involucral bracts sometimes with dark brown margins. Receptacle convex, epaleate, rarely sparsely pilose. Corolla 5-lobed. Cypselas 5-ribbed, sometimes with sessile glands, generally with myxogenic cells. Pappus a corona of free or united scales.

DISTRIBUTION. Iran, Afghanistan and C. Asia. – 21 spp.

Tanacetopsis is based on a section of *Cancrinia* described by Tzvelev (1971) and in Komarov (1961). Tzvelev transferred a number of *Tanacetum* and *Lepidolopsis* species to *Cancrinia*, although he noted that his *Cancrinia* sections could be treated as separate genera. He argued that their relationship was shown by similar floret, cypsela, and pollen morphology. The type species of *Cancrinia* (see below) is very different from *Tanacetopsis* species, in habit as well as floret and cypsela morphology. The removal of *Tanacetopsis* from *Cancrinia* is well justified (Kovalevskaja, 1972), but we doubt its status as a genus separate from *Tanacetum*, at least as presently circumscribed.

Tzvelev noted that some species of *Cancrinia*, i. e. *Tanacetopsis*, have a sparsely pilose receptacle, a character which does not occur in *Tanacetum*. Since only some species are involved, however, it cannot be used as a synapomorphy for the genus. The alleged difference in shape of involucre, also noted by Tzvelev, campanulate in *Cancrinia* and *Tanacetopsis* and cyathiform in *Tanacetum*, breaks down after examination of the numerous species involved.

Tzvelev also noted that his monotypic section *Leptanthemum* of *Pyrethrum* (*Tanacetum leptophyllum*) is almost identical to some species of *Cancrinia* sect. *Tanacetopsis* (e.g. the type species) except in being radiate rather than discoid. In fact, *Tanacetopsis* differs from *Tanacetum* simply by homogamous (discoid) as opposed to heterogamous capitula. With the inclusion of *Hemipappus* in *Tanacetum* there are also discoid representatives of *Tanacetum*. Podlech (in Podlech et al., 1986) included *Tanacetopsis* as a section of *Tanacetum*. Since we have seen only limited material of *Tanacetopsis* and since this whole *Tanacetum* group is in need of generic revision, we retain *Tanacetopsis* provisionally as a genus.

T. afghanica (Gilli) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum afghanicum* Gilli in *Feddes Reprium Spec. nov. veg.* **68:** 93 (1963) (*Tanacetum afghanicum* (Gilli) Podl.)
**T. botschantzevii* (Kovalevsk.) Kovalevsk. (*Cancrinia botschantzevii* (Kovalevsk.) Tzvelev)
T. doabensis (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum doabense* Podl., *Fl. iranica* **158**: 131 (1986).
**T. eriobasis* (Rech. f.) Kovalevsk. (*Tanacetum eriobasis* (Rech. f.) Kovalevsk.)
**T. ferganensis* (Kovalevsk.) Kovalevsk. (*Cancrinia ferganensis* (Kovalevsk.) Tzvelev)
T. freitagii (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum freitagii* Podl., *Fl. iranica* **158:** 132 (1986).
T. golovskovii (Polj.) Karmysch. (*Cancrinia golovskovii* (Polj.) Tzvelev)
T. hedgei (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum hedgei* Podl., *Fl. iranica* **158:** 130 (1986).
**T. kamelinii* Kovalevsk.
T. karataviensis (Kovalevsk.) Kovalevsk. (*Cancrinia karatavica* Tzvelev)
**T. kjurendaghii* Kurbanov
**T. krascheninnikovii* (Nevski) Kovalevsk. (*Cancrinia nevskii* Tzvelev)
T. mucronata (Regel & Schmalh.) Kovalevsk.
**T. pjataeviae* (Kovalevsk.) Karmysch. (*Cancrinia pjataeviae* (Kovalevsk.) Tzvelev)
**T. platyrachis* (Boiss.) Kovalevsk.
T. santoana (H. Kraschen., Popov & Vved.) Kovalevsk. (*Cancrinia santoana* (H. Kraschen., Popov & Vved.) Tzvelev)
**T. setacea* (Regel & Schmalh.) Kovalevsk. (*Cancrinia setacea* (Regel & Schmalh.) Tzvelev)
T. submarginata (Kovalevsk.) Kovalevsk. (*Cancrinia submarginata* (Kovalevsk.) Tzvelev)
**T. subsimilis* (Rech. f.) Kovalevsk. (*Cancrinia subsimilis*

(Rech. f.) Tzvelev, *Tanacetum subsimile* (Rech. f.) Kovalevsk.)
**T. tripinnatifida* (Oliver) Kovalevsk.
T. urgutensis (Popov) Kovalevsk. (*Cancrinia urgutensis* (Popov) Tzvelev)

18. **XYLANTHEMUM** Tzvelev in Komarov, *Fl. URSS* **26:** 877 (1961). Type species: *X. fisherae* (Aitch. & Hemsley) Tzvelev.

Shrublets generally with virgate eventually leaf-less stems, sometimes much woody basally. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, discoid or possibly also radiate with white rays. Involucral bracts in several rows, the outer much smaller than the inner. Receptacle flat, epaleate. Corolla 5-lobed. Cypselas oblong, 5–6-ribbed, generally with sessile glands and myxogenic cells. Pappus an adaxial auricle or a corona of several adaxially more developed scales.

DISTRIBUTION. Iran, Afghanistan and C. Asia. – 9 spp.

According to Tzvelev (in Komorov, 1961) *Xylanthemum* differs from *Tanacetum* by its homogamous (discoid) capitula, flat receptacle, and auriculate pappus. However, these characters occur also in *Tanacetum* with *Hemipappus* and *Spathipappus* included (see discussion under *Tanacetum*). Furthermore, *X. pamiricum* has a pappus of free scales developed more strongly on the adaxial side, probably a plesiomorphic condition when compared to the auriculate pappus in *X. fisherae*. Thus, the genus as a whole has not a pappus of a single auricle but at most, as expressed by Tzvelev, an auricle sometimes cleft to the base.

Nevertheless, it is possible that *Xylanthemum* as circumscribed by Tzvelev is a monophyletic group defined not only by these characters as synapomorphies, but also by its shrubby habit and involucral bracts in several rows. Tzvelev also stated that the species are closely related geographical-ecological races of one natural unit. Muradyan (1970) investigated fruits of *Tanacetum* and *Xylanthemum* and concluded that they are different and that *Spathipappus* belongs in *Tanacetum* rather than together with *Xylanthemum*, despite the similarity in pappus structure. The relationship of *Xylanthemum* to *Tanacetum* or probably rather to a part of *Tanacetum*, which then becomes paraphyletic by the exclusion of *Xylanthemum*, deserves further investigation. *Lepidolopha* with a similar virgate shrubby habit is clearly a related genus.

The list of species is compiled from *Flora URSS* (Komarov, 1961) with one radiate species transferred from *Pyrethrum* by Muradyan (1970) added. The position of this species, *X. tianshanicum*, within *Xylanthemum* is provisional. According to Tzvelev it is more closely related to *Trichanthemis*, and differs from that genus simply by its glabrous cypselas. Tzvelev placed it in the monotypic *Pyrethrum* section *Trichanthemopsis*. Muradyan, when investigating cypsela morphology, transferred it to *Xylanthemum* mainly because of the presence of myxogenic cells on the cypselas. In other characters, e.g. of pappus and habit, the species appears more close to *Trichanthemis* or Richteria. Podlech in Podlech et al. (1986) considers this genus as a section of *Tanacetum*.

X. fisherae (Aitch. & Hemsley) Tzvelev
X. gilletii (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum gilletii* Podl., *Fl. iranica* **158:** 140 (1986).
X. lingulatum (Boiss.) Bremer & Humphries, **comb. nov.** Basionym: *Pyrethrum lingulatum* Boiss., *Fl. orient.* **3:** 357 (1875).
X. macropodum (Hemsley & Lace) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum macropodum* Hemsley & Lace in *J. Linn. Soc.* **28:** 324 (1891).
X. paghmanense (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Tanacetum paghmanense* Podl., *Fl. iranica* **158**: 141 (1986).
X. pamiricum (Hoffm.) Tzvelev
X. polycladum (Rech. f.) Tzvelev
X. rupestre (Popov ex Nevski) Tzvelev
X. tianshanicum (H. Kraschen.) Muradyan (*Pyrethrum tianshanicum* H. Kraschen.)

19. **LEPIDOLOPHA** Winkler in *Trudy imp. S. Peterb. bot. Sada* **13:** 236 (1894). Type species: *L. komarovii* Winkler.

Shrublets with virgate, basally sometimes much woody stems. Leaves alternate or basally on the woody stems also fasciculate on brachyblasts, entire or 3-lobed. Capitula solitary or corymbose, discoid. Involucre rather narrowly urceolate; involucral bracts in 4–7 rows, the outer much smaller than the inner. Receptacle flat to convex, epaleate. Corolla 5-lobed; tube basally swollen in fruit. Cypselas oblong, 6–10-ribbed, with sessile glands. Pappus of many subulate scales.

DISTRIBUTION. C. Asia. – 9 spp.

Lepidolopha is well characterized, for example by the entire to 3-lobed leaves and the narrowly urceolate capitula with involucral bracts in several rows. The species are closely related with vicarious distributions and they differ mainly in foliage and inflorescence characters. A possibly related genus is *Xylanthemum*, also shrubby and with involucral bracts in several rows, though with a wider involucre and different pappus.

Apart from the treatment by Knorring in *Flora URSS* (Komarov, 1961), there is also a more detailed discussion by the same author (Knorring, 1959).

L. fedtschenkoana Knorr.
**L. filifolia* Pavlov
**L. gomolitzkii* Kovalevsk. & Safralieva
L. karatavica Pavlov
**L. komarovii* Winkler (*Tanacetum komarovii* (Winkler) Muradyan)
L. kraschenennikovii Kovalevsk. & Safralieva
L. mogoltavica (H. Kraschen.) H. Kraschen.
L. nuratavica H. Kraschen. (*Tanacetum nuratavicum* (H. Kraschen.) Muradyan)
**L. talasica* Kovalevsk. & Safralieva

20. **HIPPOLYTIA** Polj. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **18:** 288 (1957). Type species: *H. darvasica* (Winkler) Polj.

Pubescent, sometimes densely tomentose perennial herbs. Leaves alternate and basally more or less rosulate, much pinnatisect. Capitula densely corymbose to glomerulate or rarely solitary, discoid. Involucral bracts with dark brown margins. Receptacle flat to convex, epaleate. Corolla 5-lobed. Anthers tailed. Cypselas 5–8-ribbed, sometimes with

resin canals, with sessile glands, with a more or less distinct apical rim. Pappus absent.

DISTRIBUTION. C. Asia, Mongolia, China in Xinjiang and Tibet, and Himalaya (map by Shih, 1979: 68). – 19 spp.

Poljakov (1957) discussed the wide circumscription and loose definition of *Tanacetum* (then including also *Ajania*) and he found it difficult to accept both homogamous (discoid) and heterogamous (disciform) species in the same genus. Consequently Poljakov removed a number of central Asian discoid *Tanacetum* species to a new genus, *Hippolytia*. The cypselas have no pappus as opposed to the *Tanacetum* species. The species have a characteristic habit with much pinnatisect leaves, pedunculoid stems with crowded (rarely solitary) capitula, and involucral bracts with dark brown margins. Some high-altitude species have densely tomentose leaves crowded on vegetative shoots and short flowering stems. This alpine habit is best explained as a secondary development within the genus.

Tzvelev in *Flora URSS* (Komarov, 1961) stated that *Hippolytia* is related to *Dendranthema* and *Ajania* and that *Hippolytia* is intermediate between these genera, a view analogous to the position of '*Cancrinia*' (s. l. incl. *Tanacetopsis*) between *Pyrethrum* and *Tanacetum* s. s. According to Tzvelev radiate species of *Dendranthema* (cf. *Pyrethrum*) evolved into discoid species of *Hippolytia* (cf. *Tanacetopsis*), which further evolved into disciform species of *Ajania* (cf. *Tanacetum* s. s.).

Podlech et al. (1986) included *Hippolytia* as a section of *Tanacetum*. In our opinion *Hippolytia*, probably together with *Heliocauta*, is related to part of *Tanacetum* as discussed under *Heliocauta*. *Hippolytia* is retained here pending a reinvestigation of the whole *Tanacetum* complex. It is possible that there are species of *Ajania* that should be transferred to *Hippolytia*.

Tzvelev removed some of Poljakov's species of *Hippolytia* to *Ajania*. Shih (1979) revised the genus and added a number of Chinese species. The list of species is taken from Shih's paper but with *H. alashanensis* listed as a synonym.

H. crassicollum (Rech. f.) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum crassicollum* Rech. f. in *Biol. Skr.* **8** (2): 43 (1955) (*Tanacetum crassicollum* (Rech. f.) Podl.)
H. darvasica (Winkler) Polj.
H. delavayi (W. Smith) Shih
H. desmantha Shih
H. dolichophylla (Kitam.) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum dolichophyllum* Kitam. in *Acta. phytotax. geobot. Kyoto* **23**: 73 (1968) (*Tanacetum dolichophyllum* (Kitam.) Kitam.)
**H. glomerata* Shih
H. gossypina (C. B. Clarke) Shih
H. herderi (Regel & Schmalh.) Polj.
H. kaschgarica (H. Kraschen.) Polj. (*H. alashanensis* (Ling) Shih) – *Note*: In recent treatments of *Hippolytia* (Shih, 1979) *H. kaschgarica* has disappeared. It was based on *Tanacetum kaschgaricum* H. Kraschen. (1933) from Tien-Shan range, Mount Ischma (China in Xinjiang). Material of this species in St. Petersburg, annotated by Krascheninnikov, appears to be the species currently known as *Hippolytia alashanensis* (Ling) Shih originally described as *Tanacetum alashanense* Ling from Ala-Shan, Inner Mongolia (China). At least, they must be closely related with the shrubby, subspinose habit (see Ling, 1983: plate 13,1). Furthermore, *H. kaschgarica* which is equal to *H. alashanensis* is aberrant in *Hippolytia* and thus deserves further study.
**H. kennedyi* (Dunn) Ling
H. longifolia (Wallich) Shih (*Tanacetum himachalense* Aswal & Mehrotra)
H. megacephala (Rupr.) Polj.
**H. nana* (C. B. Clarke) Shih
H. schugnanica (Winkler) Polj.
**H. senecionis* (Besser) Polj.
**H. syncalathiformis* Shih
H. tomentosa (DC.) Tzvelev
**H. trifida* (Turcz.) Polj.
H. yunnanensis (Jeffrey) Shih

21. **HELIOCAUTA** Humphries in *Bot. Notiser* **130:** 155 (1977). Type species: *H. atlantica* (Litard. & Maire) Humphries.

A perennial rosulate or creeping herb. Leaves in a basal rosette, pinnatisect. Capitula solitary, pedunculate, discoid. Involucral bracts with dark brown margins. Receptacle conical, paleate. Corolla 5-lobed; lobes soon brownish. Style immersed in a lobed nectary. Cypselas somewhat dorsiventrally flattened, 4–5-ribbed with 2 major lateral ribs, with scattered elongated resin sacs and with an apical erose rim. Pappus absent.

DISTRIBUTION. N. Africa in Morocco. – Monotypic.

This recently described monotypic genus is difficult to place and as stated by Humphries (1977) it is not related to *Anacyclus*, wherein it was formerly classified. Humphries compared *Heliocauta* to a number of genera, notably *Achillea*, but refrained from indicating a possible sister group. The *Achillea* species discussed by Humphries, *A. barrelieri* and *A. oxyloba*, are possibly plesiomorphic within the genus and within the subtribe Achilleinae. The similarities to *Heliocauta* may be interpreted as symplesiomorphies, shared also by members of *Tanacetum*.

Another genus mentioned by Humphries is *Sclerorhachis*, supposed to have the same type of scattered epicarpic resin sacs. The elongated resin sacs in *Heliocauta* have transverse walls and are morphologically similar to the elongated rows of epicarpic myxogenic cells present in many genera. In *Sclerorhachis*, however, they are not resiniferous but myxogenic as in other genera, and a close relationship between *Heliocauta* and *Sclerorhachis* cannot be assumed.

Hippolytia is another possible relative of *Heliocauta*. They share a number of albeit homoplasious characters and can be placed together within 'Tanacetinae'. The reason for this placement is the presence of rather similar species within *Tanacetum*. It appears that both genera, singly or together, have their sister group within *Tanacetum*. One interesting species is *T. tatsienense*, a radiate species with short rays but otherwise very similar to *Heliocauta* and the single-headed species of *Hippolytia*.

4. **GONOSPERMINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Gonospermum fruticosum* (C. Smith ex Link) Less.

Frutices vel herbae perennes, basi fruticosae. Folia multilobata lobis multis rotundatis vel interdum paucilobata vel integra et margine dentata. Capitula laxe vel dense corymbosa. Receptaculum paleaceum vel raro epaleaceum. Cypselae 5–10(–12)-costatae. Pappus e squamis parvis formatus, squama quoque costam terminanti.

Shrubs or perennial, basally woody herbs. Leaves alternate, with many rounded lobes, sometimes few-lobed or entire and dentate. Capitula laxly to densely corymbose, radiate or discoid. Receptacle flat or conical to elongated, paleate or rarely epaleate. Ray floret limb white. Disc corolla 5-lobed. Cypselas 5–10(–12)-ribbed. Pappus of small scales, each terminating a rib.

DISTRIBUTION (Table 11). Canary Islands and southern Africa, mainly in Natal, one species also in Madagascar. – 3 genera, 15 spp.

Table 11 General distribution of Gonosperminae and Handeliinae and genera. x=indigenous, o=introduced.

	C.& E. Asia	SW Asia	N.Afr.	S.Afr.
Gonosperminae			x	x
Lugoa			x	
Gonospermum			x	
Inulanthera				x
Handeliinae	x	x		
Lepidolopsis	x	x		
Polychrysum	x	x		
Pseudohandelia	x	x		
Handelia	x	x		
Sclerorhachis	x			

The interesting close relationship between the two Macaronesian genera *Lugoa* and *Gonospermum* and the southern African *Inulanthera* has only recently been revealed (Källersjö, 1986). Furthermore, the southern African group of species were formerly erroneously classified in *Athanasia*, obscuring their true relationships. The Gonosperminae is probably related to a part of *Tanacetum*, in the subtribe 'Tanacetinae'. Of the two Macaronesian *Tanacetum* species, *T. ferulaceum* and *T. ptarmiciflorum*, the latter at least is a possible close relative.

Clades and characters – Fig. 5, Tables 2, 12.

Fig. 5 Cladogram of the Gonosperminae produced by the *ie* option in Hennig86. Cladogram length = 9, consistency index = 100, retention index = 100.

Clade Go1 – subtribe Gonosperminae

19 *Leaves large with many rounded lobes. Inulanthera* is very variable in leaf shape, but there are also species of *Inulanthera* with these kinds of leaves, very similar to those of *Gonospermum* and *Lugoa*.

45 *Receptacle paleate.* One species of *Inulanthera* is epaleate.

162 *Pappus of scales or teeth projected from the ribs.*

Table 12 Data matrix for the Gonosperminae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 1450576 5327181	1 1 146 23992 952295254	11 11 177555556666617 356356790567851
22. *Lugoa*	a1aa1?1	1a1000000	???0000000000000
23. *Gonospermum*	a1?a1?1	1a1111000	????????????????
24. *Inulanthera*	a1?a1?1	aa1111111	????????????????

Lugoa

There is no obvious autapomorphy for this genus.

Clade Go2

2 *Plants shrubby.*

29 *Capitula densely corymbose.*

35 *Capitula discoid.*

Gonospermum

There is no obvious autapomorphy for this genus, which appears undefined by comparison to *Inulanthera*.

Inulanthera

92 *Anthers caudate.*

95 *Anthers with endothecial tissue partly or wholly polarized.*

124 *Cypselas with 10 (8–12) multicellular epicarpic ribs.*

22. **LUGOA** DC., *Prodr.* **6:** 14 (1838). Type species: *L. revoluta* (C. Smith ex Link) DC.

A suffruticose, basally woody perennial. Leaves alternate, pinnatisect, large and flat with rounded lobes. Capitula laxly corymbose, radiate. Receptacle conical, paleate. Ray florets female, fertile; limb white. Disc corolla 5-lobed, slightly thickened at base. Cypselas 5-ribbed. Pappus of teeth projected from the ribs.

DISTRIBUTION. Canary Islands. – Monotypic.

Lugoa with radiate capitula is the most plesiomorphic member of subtribe Gonosperminae. There is no obvious autapomorphy for this monotypic genus, though the one species is clearly distinct from the species of *Gonospermum*. It is sometimes included in *Gonospermum*, but retained here in accordance with recent practice (e.g. Bramwell & Bramwell, 1974). Furthermore, inclusion of *Lugoa* in *Gonospermum* would result in a clearly paraphyletic taxon since the discoid *Gonospermum* species are more closely related to *Inulanthera* than to *Lugoa*.

23. **GONOSPERMUM** Less., *Syn. gen. Compos.*: 263 (1832). Selected type species: *G. fruticosum* (C. Smith ex Link) Less.

Rather elaborate shrubs. Leaves alternate, pinnatisect, large and flat with many rounded lobes. Capitula corymbose, discoid. Receptacle elongated, paleate. Corolla 5-lobed,

slightly thickened at base. Cypselas 5-ribbed. Pappus of scales or teeth projected from the ribs.

DISTRIBUTION. Canary Islands. – 4 spp.

Gonospermum is related to *Inulanthera* and *Lugoa*. *Inulanthera* differs by its caudate anthers and many-ribbed cypselas. By comparison to *Inulanthera*, *Gonospermum* is undefined and paraphyletic. Bramwell & Bramwell's (1974) *Wild flowers of the Canary Islands* is useful for species identification.

G. canariense (DC.) Less.
G. elegans (Cass.) DC.
G. fruticosum (C. Smith ex Link) Less.
G. gomerae Bolle

24. **INULANTHERA** Källersjö in *Nord. J. Bot.* **5:** 539 (1986). Type species: *I. calva* (Hutch.) Källersjö.

Shrubs or rarely basally woody half-shrubs. Leaves alternate, variously lobed, dentate or entire. Capitula corymbose, discoid. Receptacle flat, paleate, rarely epaleate. Corolla 5-lobed, with a narrow tube and a distinct limb. Anthers caudate; endothecial tissue polarized. Cypselas 8–10-ribbed, glabrous or sometimes glandular. Pappus of small scales or teeth, each terminating a rib.

DISTRIBUTION. S. Africa in the E. Cape, Natal, and Transvaal, and in Lesotho, Angola (*I. schistostephioides*), Zimbabwe (*I. nuda*) and Madagascar (*I. brownii*). – 10 spp.

Inulanthera is recently described and is comprised of a number of species formerly included in *Athanasia*. The species of *Inulanthera* were found to differ considerably from *Athanasia* in cypsela anatomy, having sclerenchyma of longitudinal bundles or elongated cells in the ribs rather than sclerified parenchyma cells as in *Athanasia* and lacking resin canals which are present in *Athanasia*. The species of *Inulanthera* investigated chemically also have the common polyacetylenes rather than furanosesquiterpenes, which characterize *Athanasia* and the group of related genera within the Ursiniinae. In these features *Inulanthera* is similar to most Anthemideae but the genus is further characterized by its basally caudate anthers, a very unusual character in Anthemideae (occurring elsewhere only in *Hippolytia* and *Osmitopsis*).

Cypselas with ribs projected into small pappus scales or teeth, and the characteristic leaves with many rounded leaf lobes of some species (*I. brownii*, *I. nuda*, *I. schistostephioides*) clearly indicate a relationship to *Gonospermum* and *Lugoa*. Other species have few-lobed or dentate leaves, presumably apomorphic conditions within the genus. The South African species, all occurring in Natal, are at the species level adequately described under *Athanasia* by Hilliard (1977).

I. brownii (Hochr.) Källersjö (*Athanasia brownii* Hochr.) – *Note:* Description in Hochreutiner, 1908.
I. calva (Hutch.) Källersjö (*Athanasia calva* Hutch.)
I. coronopifolia (Harvey) Källersjö (*Athanasia coronopifolia* Harvey)
I. dregeana (DC.) Källersjö (*Athanasia dregeana* (DC.) Harvey, *Athanasia punctata* (DC.) Harvey)
I. leucoclada (DC.) Källersjö (*Athanasia leucoclada* (DC.) Harvey)
I. montana (J. M. Wood & M. Evans) Källersjö (*Athanasia montana* J. M. Wood & M. Evans)
I. nuda Källersjö (*Pentzia schistostephioides* M. Taylor) – *Note:* Description in Taylor, 1940.
I. schistostephioides (Hiern) Källersjö (*Athanasia schistostephioides* Hiern) – *Note:* Description in Hiern, 1898.
I. thodei (Bolus) Källersjö (*Athanasia thodei* Bolus)
I. tridens (Oliver) Källersjö (*Athanasia tridens* Oliver)

5. **HANDELIINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Handelia trichophylla* (Schrenk) Heimerl.

Herbae perennes, basaliter suffruticosae et villosae-tomentosae, caule haud vel pauceramoso crassiusculo medulla molli. Folia alterna vel rosulata, pinnatisecta lobis filiformibus. Capitula dense vel laxe corymbosa, raro anguste paniculata, discoidea. Cypselae plerumque parvae, quinquecostatae. Pappus coroniformis e squamis parvis formatus vel nullus.

Basally more or less woody and villous-tomentose perennials with generally few- or unbranched rather thick stems with a soft pith. Leaves alternate or rosulate, pinnatisect with filiform lobes. Capitula generally small in dense to lax corymbs or rarely in a long narrow panicle, discoid. Receptacle flat to conical, paleate or epaleate. Corolla 5-lobed. Cypselas generally small and 5-ribbed, rarely slender with obtuse excrescences, sometimes with myxogenic cells. Pappus a corona of small scales or absent.

DISTRIBUTION (Table 11). Asia, mainly central part. – 5 genera, 8 spp.

This subtribe forms a homogeneous and monophyletic group, characterized by a number of synapomorphies. The relationship of *Lepidolopsis*, *Polychrysum*, *Handelia* and *Pseudohandelia* was first noted by Tzvelev (in Komarov, 1961). *Sclerorhachis* was originally part of *Anthemis*, mainly because of its paleate receptacle but after it was placed as a section of *Anthemis* (Rechinger, 1944) Rechinger elevated it to generic rank of uncertain position within the tribe (Rechinger 1968). We consider that *Sclerorhachis* is related to *Handelia* and *Pseudohandelia* and a true member of this subtribe. This relationship has probably been obscured by the distinct habit of *Sclerorhachis*, with basal leaf-rosettes and laxly branched, leafless aerial stems. We interpret these stems as branches of a secondarily lax inflorescence, homologous to the dense corymbs of the other genera.

From the data matrix there is only one parsimonious solution to the generic interrelationships within Handeliinae, shown in the cladogram. The sister group of Handeliinae is probably to be found within *Tanacetum*, where there are several thick-stemmed species with corymbose inflorescences.

Clades and characters – Fig. 6, Tables 2, 13.

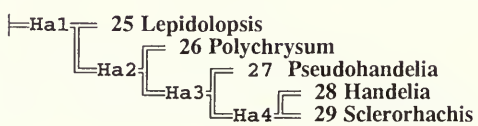

Fig. 6 Cladogram of the Handeliinae produced by the *ie* option in Hennig86. Cladogram length = 13, consistency index = 92, retention index = 80.

Table 13 Data matrix for the Handeliinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111	111	1111 11
	1450576	13323701457	1555556666617775674
	5327181	865190293511	3356790567851560606
25. *Lepidolopsis*	a1?a1?1	111100000000	????????????????00p
26. *Polychrysum*	a1?a1?1	111011000000	????????????????000
27. *Pseudohandelia*	a1?a1?1	111010111000	????????????????p
28. *Handelia*	a1?a1?1	111010100a00	????????????????0??p
29. *Sclerorhachis*	a1?a1?1	1a1000100aa1	????????????????0??0

Clade Ha1 – subtribe Handeliinae

8 *Plants basally villous-tomentose with rather thick stems and a soft pith.*

16 *Leaves much pinnatisect with filiform lobes.*

35 *Capitula discoid.*

Lepidolopsis

31 *Capitula in a long narrow panicle or raceme.*

Clade Ha2

29 *Capitula densely corymbose.* In *Sclerorhachis* the capitula are terminal on the loosely branched, leafless aerial stems, which are considered homologous to the branches of a corymbose inflorescence.

Polychrysum

30 *Capitula very small and numerous in a large, dense, semiglobose corymb.*

Clade Ha3

172 *Pappus absent in ray and disc cypselas.*

Pseudohandelia

109 *Cypselas arcuate.*

113 *Cypselas slender and tuberculate with numerous obtuse excrescences.*

Clade Ha4

45 *Receptacle paleate.*

Handelia

There is no obvious autapomorphy for this genus.

Sclerorhachis

29 reversed. See clade Ha1.

51 *Floral parts with resin canals.*

71 *Corolla apically contracted.*

25. **LEPIDOLOPSIS** Polj. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **19:** 374 (1956). Type species: *L. turkestanica* (Regel & Schmalh.) Polj.

A basally woody perennial with rather thick unbranched stems with a soft pith, villous-tomentose at base and the leaf bases. Leaves alternate, much pinnatisect with filiform lobes. Capitula small, numerous in a long panicle, discoid. Receptacle conical, epaleate. Corolla 5-lobed, with sessile glands. Cypselas small, 5-ribbed. Pappus of several mainly abaxial acute scales.

DISTRIBUTION. Iran, Afghanistan and C. Asia. – Monotypic.

Vegetatively *Lepidolopsis* is very similar to *Polychrysum*, *Handelia* and *Pseudohandelia*. All four genera have single, unbranched or apically few-branched, basally pubescent stems with much pinnatisect leaves with filiform lobes. *Lepidolopsis* differs by its much elongated inflorescence and its sessile floret glands. Originally Poljakov included a number of discoid species in *Lepidolopsis*. These are now in other genera, mainly *Tanacetum* and *Tanacetopsis*. Both *Polychrysum tadshikorum* and *Pseudohandelia umbellifera* were also classified in *Lepidolopsis* by Poljakov.

26. **POLYCHRYSUM** (Tzvelev) Kovalevsk. in Vvedensky, *Fl. uzbekistana* **6:** 148 (1962). Type species: *P. tadshikorum* (Kudr.) Kovalevsk. – *Cancrinia* sect. *Polychrysum* Tzvelev.

A basally woody perennial, one to few-branched with rather thick light stems and a soft pith, villous-tomentose at the leaf bases. Leaves alternate, much pinnatisect with filiform lobes. Capitula small, numerous in a large, dense, semiglobose corymb, discoid. Receptacle convex, epaleate. Corolla 5-lobed, with stalked glands. Cypselas small, 5-ribbed, with stalked glands. Pappus a corona of many small scales.

DISTRIBUTION. Afghanistan, C. Asia. – Monotypic.

Polychrysum is based on a monotypic section of *Cancrinia*, described by Tzvelev in *Flora URSS* (Komarov, 1961). It is clearly different from the type species of *Cancrinia*, and more closely related to *Lepidolopsis*, *Handelia* and *Pseudohandelia*. One character stressed by Tzvelev is the capitulum with only one mature fruit. This is obviously correlated to the small and numerous capitula.

27. **PSEUDOHANDELIA** Tzvelev in Komarov, *Flora URSS* **26:** 878 (1961). Type species: *P. umbellifera* (Boiss.) Tzvelev.

A basally woody perennial with unbranched, rather thick stems with a soft pith, villous-tomentose at the stem and leaf bases. Leaves alternate, basally approaching rosulate, much pinnatisect with filiform lobes. Capitula corymbose, discoid. Receptacle conical, epaleate. Corolla 5-lobed, with many stalked glands. Cypselas slender and somewhat arcuate, with 5 vascular strands, tuberculate with numerous obtuse excrescences. Pappus absent.

DISTRIBUTION. Iran, Afghanistan, C. Asia and China in Xinjiang. – Monotypic.

Pseudohandelia and *Handelia* are very similar and closely related. Their close relationship has been more or less concealed by the traditional practice of keeping taxa with and without receptacular paleae far apart in classification. The two genera are often confused. Apart from the receptacle character *Pseudohandelia* is also distinguished by its slender and tuberculate cypselas and the more dense, umbelliform corymb. The close relationship of *Pseudohandelia* to *Handelia* as well as to *Polychrysum* (treated by Tzvelev as a section of *Cancrinia*), and *Lepidolopsis* was first noted by Tzvelev (in Komarov, 1961).

The cypsela excrescences are homologous with gland stalks; glands with such stalks are present on the corolla.

28. **HANDELIA** Heimerl in *Ost. bot. Z.* **71**: 215 (1922). Type species: *H. trichophylla* (Schrenk) Heimerl.

A basally woody perennial with few- or unbranched, rather thick stems with a soft pith, basally and at the leaf bases villous-tomentose. Leaves alternate, basally becoming almost rosulate, leaves pinnatisect, with deep sinuses and filiform lobes. Capitula small, numerous, corymbose, discoid. Receptacle conical, paleate. Corolla 5-lobed, with stalked glands. Cypselas small, 5-ribbed, with an abaxial rim. Pappus absent.

DISTRIBUTION. Afghanistan, Pakistan, C. Asia and China in Xinjiang. – Monotypic.

Handelia is very similar to and closely related to *Pseudohandelia*, though the two genera have been placed far apart. *Handelia* has a paleate receptacle, whereas *Pseudohandelia* is epaleate. They are often confused but they are easily distinguished by the receptacle character and by their different cypselas. *Handelia* also has a more laxly branched inflorescence than *Pseudohandelia*. The relationship to *Sclerorhachis* is discussed below.

29. **SCLERORHACHIS** (Rech. f.) Rech. f. in *Anz. öst. Akad. Wiss. Mathematische Naturwissenschaftliche Klasse* **105**: 242 (1968). Type species: *S. caulescens* (Aitch. & Hemsley) Rech. f. – *Anthemis* sect. *Sclerorhachis* Rech. f.

Rosulate basally pubescent perennials with a basal leaf-rosette and almost naked, loosely branched stems, basally rather thick and with a soft pith. Leaves pinnatisect, with a persistent, sclerified rachis. Capitula laxly corymbose, pedunculate, discoid. Receptacle flat to convex, paleate; paleae filiform. Corolla 5-lobed, with a distinct, apically contracted limb. Cypselas 5-ribbed, with scattered rows of myxogenic cells. Pappus absent.

DISTRIBUTION. Iran and Afghanistan. – 4 spp.

The type species of *Sclerorhachis* was originally placed in *Anthemis*, though considered highly isolated (Rechinger, 1944). At a first glance *Sclerorhachis* seems isolated but it is a member of subtribe Handeliinae together with *Handelia* and *Pseudohandelia* (Rechinger, 1955, 1968). In *Sclerorhachis* the leaves are concentrated into a basal leaf-rosette and we consider the loosely branched, leafless aerial stems with terminal capitula homologous to the corymbose inflorescence of the other genera. The receptacle is furnished with filiform bristles in the same position as receptacular paleae, hence they appear homologous to paleae.

S. caulescens (Aitch. & Hemsley) Rech. f. (*Anthemis caulescens* Aitch. & Hemsley)
**S. leptoclada* Rech. f.
S. platyrhachis (Boiss.) Podl. ex Rech. f.
S. polysphaera Rech. f.

6. **ARTEMISIINAE** Less. emend. Bremer & Humphries, **emend. nov.**

Lessing in *Linnaea* **5**: 163 (1830) ('Artemisieae'). Type species: *Artemisia vulgaris* L.

Herbae annuae vel perennes, suffrutices vel frutices. Capitula interdum radiata, saepe disciformia vel discoidea, corymbosa vel paniculata. Receptaculum plerumque epaleaceum. Appendix apicalis antherarum subtriangularis vel lanceolato-linearis, parietibus cellularum aliquantum incrassatis. Cypselae oblongo-obovoideae, quinque-costatae vel saepe obovoideae ecostatae, parietibus tenuibus, raro pilosae. Pappus nullus vel raro coroniformis e squamis parvis formatus.

Perennial, rarely annual herbs, half-shrubs or shrubs; indumentum frequently of dolabriform hairs. Leaves variously dissected, rarely entire. Capitula radiate or generally disciform or discoid, often rather small; inflorescence various but often corymbose or paniculate. Receptacle epaleate or very rarely paleate. Ray floret limb white, yellowish or pink. Outer florets (in disciform capitula) in one row (rarely two), female, fertile. Disc or central florets perfect and hermaphrodite or female-sterile, 5-lobed. Apical anther appendages (sub)triangular-lanceolate-linear, of rather thick-walled cells. Pollen often without or with short spines. Cypselas oblong-obovoid, 5-ribbed or generally rather small, obovoid and faintly ribbed or without ribs, thin-walled, with or without myxogenic cells in rows, rarely pilose. Pappus absent or very rarely coroniform, of small scales.

DISTRIBUTION (Table 14). Worldwide but mainly northern hemisphere and especially central and E. Asia, some *Artemisia* species widespread as weeds. – 18 genera, 634 spp.

The main genera of this subtribe are familiarly known as the *Artemisia* group, including the large genera *Artemisia* and *Seriphidium* (commonly considered a section of *Artemisia*), eight small Asian genera, and two small North American genera. The group is characterized by disciform or discoid, commonly paniculate capitula, smooth or short spined pollen, and obovoid, thin-walled, and ribless cypselas without a pappus.

However, within this subtribe we have included the probable, more plesiomorphic relatives of the *Artemisia* group (Fig. 7, Clades Ar1-Ar5), which in previous classifications were hidden within a broad concept of *Chrysanthemum*. These relatives include the radiate genera *Brachanthemum*, *Dendranthema*, *Arctanthemum* and *Tridactylina* with solitary or laxly corymbose capitula, and the disciform *Ajania* and *Phaeostigma* with densely corymbose capitula. These genera have rather thin-walled and more or less faintly ribbed cypselas always without a pappus. The apical anther appendages are synapomorphic for the whole subtribe. They are (sub)triangular to lanceolate-linear, often acute to acuminate, and composed of rather thick-walled cells, best expressed in the apomorphic representatives of the *Artemisia* group.

The sister group of Artemisiinae is to be found within *Tanacetum*, where there are species very similar to representatives of *Dendranthema* and *Brachanthemum*. The delimitation between *Tanacetum* and these two genera, notably *Dendranthema*, traditionally rests on two characters, presence of pappus and myxogenic cells on the cypselas. Pappose species without myxogenic cells are classified in *Tanacetum*

Table 14 General distribution of Artemisiinae and genera. x=indigenous, o=introduced.

	N. Am.	Eur-Asia	C. & E. Asia	SW Asia	S. Eur.	N. Afr.	S. Afr.	Austr. N. Zeal.	S. Am.
Artemisiinae	x	x	x	x	x	x	x	o	x
Brachanthemum			x						
Dendranthema		x	x						
Arctanthemum		x	x	x					
Tridactylina			x						
Ajania			x						
Phaeostigma			x						
Stilpnolepis			x						
Ajaniopsis			x						
Filifolium			x						
Sphaeromeria	x								
Kaschgaria			x						
Seriphidium	x	x	x	x	x				
Crossostephium				x					
Artemisia	x	x	x	x	x	x	x	o	x
Neopallasia			x						
Turaniphytum			x						
Mausolea			x						
Picrothamnus	x								

and epappose species with or without myxogenic cells are classified in *Dendranthema*. (Pappose species with myxogenic cells represent another problem, and are more or less provisionally relegated to other genera, as exemplified by *Xylanthemum tianshanicum*). The relationship of *Dendranthema* and Artemisiinae in general to *Tanacetum* cannot be assessed in detail before the latter genus has been properly revised and dismantled.

The cladogram (Fig. 7) is one of many (71) equally parsimonious trees. In this case the analysis was performed with characters 29 and 31 combined into one multistate character with two apomorphic states, densely corymbose and paniculate-racemose capitula. A preliminary analysis with the binary characters as presented in the matrix (Table 15) yielded an artificial grouping of *Stilpnolepis* and *Seriphidium* supported by a reversal in character 29, i.e. loss of the dense capitula corymbs, but the two genera are totally different in inflorescence structure. The strict consensus tree of all the equally parsimonious cladograms is almost totally collapsed, indicating the instability in our current hypothesis of Artemisiinae generic interrelationships. However, clade Ar2 with *Dendranthema*, *Arctanthemum* and *Tridactylina*, as well as clade Ar10, *Mausolea* and *Picrothamnus*, were supported by all cladograms and hence retained in the consensus tree.

Clades and characters – Fig. 7, Tables 2, 15.

Clade Ar1 – subtribe Artemisiinae

11 *Plants with dolabriform hairs.* Dolabriform, i.e. T-shaped, or Y-shaped hairs occur in most genera of this subtribe. They are also frequent in Leucantheminae, *Anthemis* (Anthemidinae) and some genera of Achilleinae. The character is possibly a synapomorphy at a lower level within the tribe.

93 *Anthers with triangular-linear-lanceolate apical appendages, of rather thick-walled cells.* This character is present in all genera, though variously expressed.

172 *Pappus absent in ray and disc cypselas. Crossostephium* and one species of *Sphaeromeria* both have a pappus of short scales.

Brachanthemum

2 *Plants shrubby.* In Artemisiinae there are many transitions from woody perennials to half-shrubs or shrubs. Hence the character is difficult to apply and it is present within several genera not scored in the matrix.

Clade Ar2

44 *Involucral bracts with dark brown margins.* This character is present also within *Ajania*, *Phaeostigma*, and *Tanacetum*, where the sister group of the subtribe is found. Hence the character may be plesiomorphic within the subtribe.

Dendranthema

This genus is plesiomorphic compared to *Arctanthemum*, *Tridactylina* and possibly also compared to the rest of the subtribe.

Arctanthemum

6 *Plants rhizomatous with rosulate, spathulate-obovate-linear leaves.*

15 reversed. *Leaves not variously deeply lobed or divided, but entire.*

Tridactylina

1 *Plants annual.*

52 reversed. *Ray floret limb not white, but yellow.* There are several species of *Dendranthema* with yellow rays.

Clade Ar3

29 *Capitula densely corymbose.* Inflorescences are variable and complicated in subtribe Artemisiinae. Most of the *Artemisia* group of genera have paniculate inflorescences. In *Stilpnolepis* the capitula are, probably secondarily, solitary or laxly corymbose.

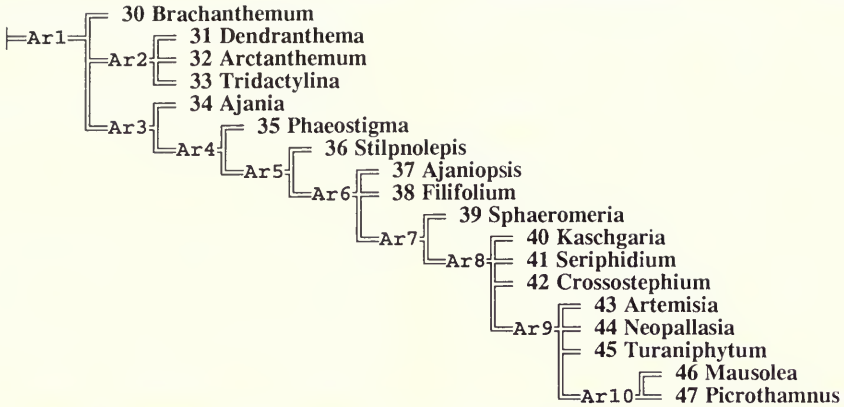

Fig. 7 Cladogram (of 71 possible) of the Artemisiinae produced by the *bb* option in Hennig86. Cladogram length = 48, consistency index = 79, retention index = 82.

Table 15 Data matrix for the Artemisiinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 1 11 1 1 111 1111 11 11
	1450576 197 4 2390536974131831291693670046 6 8 5677755556175531 147 46788
	5327181 1322461966245578331208629761249468783 1 0605635790516174465798322 3
30. *Brachanthemum*	a1aa1?1 a1110000000p0000?0p000000000000000000 ?????000000000000000000000
31. *Dendranthema*	a1aa111 a110a00p000000000?000000000000000000 ?????000000000000000000000
32. *Arctanthemum*	01111?1 a1101100000000000?000000000000000000 ???000000000000000000000
33. *Tridactylina*	a1?a1?1 ?1101010000000000?000000000000000000 ?????000000000000000000000
34. *Ajania*	a1?a1?1 a110p00a10p000000?000000000000000000 ?????????????pp00000000000
35. *Phaeostigma*	a1?a1?1 a110p001111000000?000000000000000000 ?????????????000000000000
36. *Stilpnolepis*	a1?a1?1 ?11000p0010111?p00?00000000?0000000??00 ?????????????p0p0000000000
37. *Ajaniopsis*	a1?a1?1 ?1100011110101110?000000000000000000 ?????????????000000000000
38. *Filifolium*	a1?a1?1 a1100001110101101?000000000000000000 ?????????????000000000000
39. *Sphaeromeria*	a1?a1?1 a110000a11010110010p000000000000000p ?????????????000p000000000
40. *Kaschgaria*	a1?a1?1 a1100000110101100?111000000000000000 ?????????????000000000000
41. *Seriphidium*	a1?a1?1 a11p00p001011?1001a0011000?0000000??00 ?????????????0p00ppp000000
42. *Crossostephium*	a1?a1?1 ?1010000110001100?100001000000000000 ?00?????????000000000000
43. *Artemisia*	a1?a111 a11pp0p0110101100aap0000100000ppp00p0 ?????????????0p0pp00ppppp
44. *Neopallasia*	a1?a1?1 a11000a0110101100?100000111100000000 ?????????????0000p00000000
45. *Turaniphytum*	a1?a1?1 ?1100000110101100?100000100011100000000 ?????????????000000000000
46. *Mausolea*	a1?a1?1 a1110000110101100?100000100000001111100 ?????????????000000000000
47. *Picrothamnus*	a1?a1?1 a1110000110101100110000010000000111001 1 ?????????????000000000000

36 *Capitula disciform. Stilpnolepis* and *Seriphidium* have discoid capitula. Within this subtribe discoid capitula are most parsimoniously interpreted as derived from disciform, rather than from radiate capitula.

Ajania

There is no autapomorphy for this genus, which appears to be a paraphyletic grade when compared to *Phaeostigma* and the *Artemisia* group.

Clade Ar4

96 *Pollen grains with short spines or without spines.*

Phaeostigma

102 *Style-branches brownish.*

Clade Ar5 – the *Artemisia* group

154 *Cypselas thin-walled, obovoid to oblanceolate, devoid of ribs.* Faint ribs are sometimes present, most clearly seen in *Crossostephium* and sometimes within *Sphaeromeria.*

Stilpnolepis

29 reversed. See clade Ar3.

35 *Capitula discoid.* See character 36 under clade Ar3.

Clade Ar6

65 *Outer female floret corollas 'flask-shaped', tapering above or narrowly cylindrical.*

97 *Pollen grains without spines.*

Ajaniopsis

1 *Plants annual.*

78 *Corolla apically with erect, straight hairs.*

Filifolium

143 *Cypselas with myxogenic glands in 2 distinct adaxial-lateral rows.*

Clade Ar7

13 *Plants with interxylary cork.* Interxylary cork has been studied in *Sphaeromeria*, *Seriphidium*, *Artemisia* and *Picrothamnus* only.

Sphaeromeria

There is no obvious autapomorphy for this genus.

Clade Ar8

29 reversed. See clade Ar3.

31 *Capitula in a long narrow panicle or raceme.* See character 29 under clade Ar3.

Kaschgaria

12 *Plants with stellate hairs.*

80 *Corolla apically with stellate hairs.*

Seriphidium

35 *Capitula discoid.* See character 36 under clade Ar3.

38 *Involucral bracts in 4–7 rows.*

116 *Disc cypselas laterally flattened.*

Crossostephium

2 *Plants shrubby.* See note under *Brachanthemum*.

22 *Leaves entire or apically tridentate.*

154 reversed. See clade Ar5.

172 reversed. See clade Ar1.

Clade Ar9

99 *Style slender, parallel-sided at base.*

Artemisia

There is no autapomorphy for *Artemisia* when compared to the remaining four genera.

Neopallasia

1 *Plants annual.*

17 *Leaves pectinate-pinnatisect with filiform, apically somewhat swollen and mucronulate lobes.*

66 *Outer female floret corollas without teeth.*

91 *Central florets of two kinds; outer perfect, inner completely sterile with reduced ovaries.*

Turaniphytum

32 *Capitula in glomerules arranged in long spikes.*

64 *Outer female florets subtended by scaphoid bracts.*

79 *Corolla apically with long, reddish hairs.*

Clade Ar10

2 *Plants shrubby.* See note under *Brachanthemum*.

104 *Disc floret style-branches fused.* This is characteristic also of *Artemisia* sect. *Dracunculus*.

106 *Central floret ovaries reduced; florets functionally male.*

148 *Cypselas cobwebby pilose.*

Mausolea

67 *Outer female florets without corollas.*

68 *Outer female floret style-branches lanceolate, flat, acute.*

Picrothamnus

3 *Plants spiny.*

81 *Corolla cobwebby pilose.*

30. **BRACHANTHEMUM** DC., *Prodr.* **6:** 44 (1838). Type species: *B. fruticulosum* (Ledeb.) DC.

Small, more or less procumbent shrublets, woody at the base. Leaves alternate, few-lobed. Capitula solitary or laxly corymbose, pedunculate, radiate or rarely discoid. Receptacle flat or convex to conical, epaleate. Ray florets female, fertile; limb yellow or yellowish. Disc corolla 5-lobed; tube with sessile glands. Apical anther appendage subtriangular. Cypselas obovoid to oblong, faintly 5-7-ribbed, thin-walled, with myxogenic cells. Pappus absent.

DISTRIBUTION. C. Asia, Mongolia and China (map by Krascheninnikov, 1949: 199). – 10 spp.

According to Krascheninnikov (1949) and Tzvelev (in Komarov, 1961) most species of *Brachanthemum* are closely related, although *B. baranovii* is different and placed in the monotypic sect. *Dendranthemopsis*. It differs from sect. *Brachanthemum* by its oblong rays and flat, shortly pilose receptacle, as opposed to the otherwise shorter rays and convex to conical, glabrous receptacle. On the other hand the characteristic shrubby habit, the few-lobed leaves, and the rather small, cyathiform to urceolate capitula may distinguish this genus as monophyletic. Tzvelev noted the close relationship to *Dendranthema*, emphasized also by the similar thin-walled, myxogenic fruits without a pappus (described in detail by Savczenko, 1949). The list of species is taken from Krascheninnikov's (1949) revision and *Flora URSS* (Komarov, 1961) with species from China and Mongolia added.

**B. baranovii* (H. Kraschen. & Polj.) H. Kraschen.
B. fruticulosum (Ledeb.) DC.
B. gobicum H. Kraschen.
B. kasakhorum H. Kraschen.
B. kirghisorum H. Kraschen.
**B. krylovii* Serg.
B. mongolicum H. Kraschen.
**B. mongolorum* Grubov
B. pulvinatum (Hand.-Mazz.) Shih (*B. nanshanicum* H. Kraschen.)
B. titovii H. Kraschen.

31. **DENDRANTHEMA** (DC.) Des Moul. in *Act. Soc. linn. Bordeaux* **20:** 561 (1860). Type species: *D. indicum* (L.) Des Moul. – *Pyrethrum* sect. *Dendranthema* DC.

Perennial herbs or half-shrubs. Leaves alternate, pinnatisect, lobed, serrate or rarely entire. Capitula laxly corymbose or solitary, radiate. Involucral bracts generally with dark brown margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white, pink, or yellowish. Disc corolla 5-lobed; tube generally with sessile glands. Apical anther appendage subtriangular. Cypselas obovoid, faintly 5–8-ribbed, thin-walled, generally with myxogenic cells in rows. Pappus absent.

DISTRIBUTION. Asia, mainly in China and Japan, one species extending to E. Europe (*D. zawadskii*). – 37 spp.

Dendranthema differs from *Tanacetum* (i.e. *Chrysanthemum*

s. l.) by its obovoid, thin-walled, generally myxogenic cypselas without a pappus. It was revised by Tzvelev (in Komarov, 1961). Later Tzvelev (1985) transferred three species of *Dendranthema* to a new genus *Arctanthemum* and later erected the new genus *Hulteniella* based on *Arctanthemum integrifolium* (Richardson) Tzvelev (Tzvelev, 1987). Other related genera are *Brachanthemum* and *Tridactylina*.

There is still much work to be undertaken on this species-rich and horticulturally interesting genus. There are many, poorly understood species, known only from the original description, and probably several undescribed ones. Possibly there are other species to be transferred from *Tanacetum*. Future revision should be undertaken with *Ajania*, since some species of *Dendranthema* may be more closely related to *Ajania* than to other species within *Dendranthema*. In other words, *Dendranthema* may be paraphyletic when *Ajania* and its relatives (i.e. *Artemisia* etc.) are excluded. As presently understood, *Dendranthema* is always radiate and *Ajania* always disciform. Most species of *Dendranthema* also have involucral bracts with dark brown margins, a character that may have been secondarily lost in the small-headed species of *Ajania*.

The well-known autumn-flowering chrysanthemums of horticulture are derived from *D. grandiflorum* and *D. indicum*.

The list of species is compiled mainly from *Flora URSS* (Komarov, 1961) and the *Flora of the People's Republic of China* (Ling & Shih, 1980, 1983; Shih & Fu, 1983), as well as from accounts from Japan by Kitamura (1940, 1978, 1979). These authors transferred a number of species from *Chrysanthemum* to *Dendranthema*. Kitamura also included four disciform species, *D. pallasianum*, *D. rupestre*, *D. pacificum*, and *D. shiwogiku*, in section *Ajania*. The latter we consider as a separate genus in agreement with various other authors and so the disciform species are here listed under *Ajania*. The generic distinction, as discussed under that genus, is in doubt but pending a detailed study of both genera we consider it best to transfer a few disciform Japanese *Dendranthema* species to *Ajania* rather than to recombine the numerous Chinese *Ajania* species under *Dendranthema*.

**D. aphrodite* (Kitam.) Kitam. Japan.
**D. argyrophyllum* (Ling) Ling & Shih. China.
D. arisanense (Hayata) Ling & Shih. Taiwan.
D. boreale (Makino) Ling ex Kitam. China, Korea, Japan.
D. chalchingolicum (Grubov) Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum chalchingolicum* Grubov in *Bot. Zhurn.* **15**: 1592 (1972). Mongolia.
D. chanetii (A. Léveillé) Shih (*D. erubescens* (Stapf) Tzvelev). China, Korea.
D. coreanum (A. Léveillé & Vaniot) Vorosch. Korea.
**D. crassum* (Kitam.) Kitam. Japan.
D. cuneifolium (Kitam.) Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum cuneifolium* Kitam. in *Acta phytotax. geobot. Kyoto* **7**: 68 (1938). Japan.
**D. dichrum* Shih. China.
**D. glabriusculum* (W. Smith) Shih. China.
D. grandiflorum (Ramat.) Kitam. (*D. morifolium* (Ramat.) Tzvelev). China, much cultivated.
D. hypargyrum (Diels) Ling & Shih. China.
D. indicum (L.) Des Moul. China, Korea, Japan, much cultivated.
D. japonense (Nakai) Kitam. Japan.
D. japonicum (Makino) Kitam. Japan.
D. lavandulifolium (Fischer ex Trautv.) Kitam. China.
**D. littorale* (Mackawa) Tzvelev. Far East, Japan.
D. maximowiczii (V. Komarov) Tzvelev. Far East, China, Korea.
D. miyatojimense (Kitam.) Hind. Japan.
D. mongolicum (Ling) Tzvelev. E. Siberia, China.
**D. morii* (Hayata) Kitam. Taiwan.
D. nankingense (Hand.-Mazz.) Y. R. Ling. China.
**D. okiense* (Kitam.) Kitam. Japan.
D. oreastrum (Hance) Ling (*D. sichotense* Tzvelev). Far East, China, Korea.
D. ornatum (Hemsley) Kitam. Japan.
**D. parvifolium* (Chang) Shih. China.
D. potentilloides (Hand.-Mazz.) Shih. China.
**D. rhombifolium* Ling & Shih. China.
**D. sinchangense* (Ueki) Kitam. Korea.
D. sinuatum (Ledeb.) Tzvelev. C. Asia, Mongolia.
**D. vestitum* (Hemsley) Ling. China.
**D. weyrichii* (Maxim.) Tzvelev. Far East, Japan.
**D. xeromorphum* Khokr. Russia.
D. yezoense (T. Maek.) Hind. Japan.
D. yoshinaganthum (Makino ex Kitam.) Kitam. Japan.
D. zawadskii (Herbich) Tzvelev (*D. naktongense* (Nakai) Tzvelev). From E. Europe through Russia to China, Mongolia, and Japan.

32. **ARCTANTHEMUM** (Tzvelev) Tzvelev in *Nov. Sist. Vysshikh Rast.* **22:** 274 (1985). Type species: *A. arcticum* (L.) Tzvelev (including *Hulteniella* Tzvelev).

Perennial rhizomatous herbs. Leaves rosulate to alternate, obovate-spathulate to linear, apically lobed-serrate or entire. Capitula solitary, radiate. Involucral bracts with dark brown margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white. Disc corolla 5-lobed; tube generally with sessile glands. Apical anther appendage subtriangular. Cypselas oblong, somewhat 5–8-ribbed, without myxogenic cells. Pappus absent.

DISTRIBUTION. Arctic Eurasia, Siberia, Far East, Japan, Arctic N. America. – 4 spp.

Arctanthemum was formerly a section of *Dendranthema*. It consists of more or less rosulate herbs with an arctic distribution, whereas most *Dendranthema* species are leafy herbs or herbaceous perennials from China and Japan. It is worth noting that Tzvelev (1987) transferred *A. integrifolium* to a new genus, *Hulteniella* Tzvelev, which we do not recognize here.

A. arcticum (L.) Tzvelev (*Dendranthema arcticum* (L.) Tzvelev). Far East and Arctic America.
A. hultenii (A. & D. Löve) Tzvelev (*Dendranthema hultenii* (A. & D. Löve) Tzvelev). Arctic Eurasia and Arctic America.
A. integrifolium (Richardson) Tzvelev (*Dendranthema integrifolium* (Richardson) Tzvelev, *Hulteniella integrifolium* (Richardson) Tzvelev). NE Siberia and Arctic N. America.
A. kurilense (Tzvelev) Tzvelev (*Dendranthema kurilense* (Tzvelev) Tzvelev). Far East, Japan.

33. **TRIDACTYLINA** (DC.) Schultz-Bip. in Webb & Berthelot, *Hist. nat. Iles Canaries* **3** (2,2): 245 (1844). Type species: *T. kirilowii* (Turcz. ex DC.) Schultz-Bip.

An annual herb. Leaves alternate, few-lobed. Capitula laxly corymbose, radiate. Involucral bracts with dark brown margins. Receptacle flat to convex, epaleate. Ray florets neuter; limb yellow. Disc corolla 5-lobed. Apical anther appendage subtriangular. Cypselas 5-ribbed, with myxogenic cells and with an apical rim. Pappus absent.

DISTRIBUTION. E. Siberia. – Monotypic.

According to Tzvelev in *Flora URSS* (Komarov, 1961) this species is clearly related to *Dendranthema* but differs by its annual habit and neutral rays. It is similar for example in foliage to some species of *Dendranthema* and *Arctanthemum*.

34. **AJANIA** Polj. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **17:** 419 (1955). Type species: *A. pallasiana* (Fischer ex Besser) Polj.

Perennial herbs or half-shrubs. Leaves alternate, pinnatisect, lobed, serrate, or rarely entire. Capitula small, corymbose or rarely solitary, disciform. Receptacle convex to conical, epaleate. Outer female florets in one row. Corollas of central florets 5-lobed; tube generally with sessile glands. Apical anther appendage subtriangular. Cypselas obovoid, faintly 4–6-ribbed, thin-walled, generally with myxogenic cells in rows. Pappus absent.

DISTRIBUTION. C. Asia, mainly in China, also in Japan. – 34 spp.

Poljakov removed a number of species from *Artemisia* to a separate genus *Ajania*. He noted that *Ajania* has fertile florets and the common form of distinct 5-lobed corollas with spreading lobes, whereas in *Artemisia* only some of the florets in each capitulum are fertile, producing mature fruits, and the corollas have small erect lobes. *Ajania* also has a corymbose inflorescence as opposed to the elongated inflorescences of *Artemisia*. Poljakov speculated that *Ajania* is a very old group derived from the same ancestors as *Artemisia*.

Tzvelev (in Komarov, 1961) accepted *Ajania* although he retained some of Poljakov's *Ajania* species in *Artemisia*. He also noted the close affinity between *Dendranthema* and *Ajania*, and speculated that *Ajania* and *Artemisia* are two convergent and habitually similar lines independently evolved from the same 'dendranthemoid' ancestors. More parsimoniously, *Ajania* may be considered the plesiomorphic sister group to *Artemisia* and all its relatives. Possibly *Ajania* or part of the genus is the sister group of *Artemisia* and the other genera with smooth or short-spined pollen, as indicated in the cladogram. *Dendranthema* is even more plesiomorphic and possibly paraphyletic with *Ajania*, and *Artemisia* etc. excluded. *Ajania* differs from *Dendranthema* by its smaller, disciform, densely corymbose capitula. No doubt this species-rich and little-known genus deserves a detailed study together with *Dendranthema*.

A few species of *Ajania* have recently been placed in a separate genus, *Phaeostigma*. There may be several species of *Ajania* (Muldashev, 1982, 1983) that should be transferred to *Phaeostigma*, should the latter be kept distinct. The type species of *Ajania*, *A. pallasiana*, and *A. latifolia*, *A. rupestris*, and *A. shiwogiku* are all examples of species similar to *Phaeostigma*. The matter is discussed further under *Phaeostigma*.

Tzvelev suspected that the distinction between *Ajania* and *Dendranthema* would become difficult after examination of the extensive Chinese material. Nevertheless Ling & Shih (1980, 1983) kept them separate in their accounts of the Chinese species. Our list of species is compiled mainly from their treatments and from *Flora URSS* (Komarov, 1961). The species from Tibet were listed by Shih & Fu (1979) and the Japanese species are from Kitamuras's (1978) *Dendranthema* sect. *Ajania* (see discussion under *Dendranthema*).

A. achilleoides (Turcz.) Polj. ex Grubov. Mongolia.
A. adenantha (Diels) Ling & Shih. China.
**A. brachyantha* Shih. China.
A. breviloba (Franchet ex Hand.-Mazz.) Ling & Shih. China.
**A. elegantula* (W. Smith) Shih. China.
A. fastigiata (Winkler) Polj. C. Asia, China.
A. fruticulosa (Ledeb.) Polj. (*A. aureoglobosa* (W. Smith & Farrer) Muld.). C. Asia, E. Siberia, Mongolia, China.
A. gracilis (Hook. f. & Thomson) Polj. ex Tzvelev. C. Asia, China, Himalaya.
**A. grubovii* Muld. Mongolia.
**A. junnanica* Polj. China.
A. khartensis (Dunn) Shih (*A. mutellina* (Hand.-Mazz.) Muld.). China.
**A. kokanica* (H. Kraschen.) Tzvelev. C. Asia.
A. latifolia Shih. China.
A. myriantha (Franchet) Ling ex Shih (*A. oresbia* (W. Smith) Muld.). China.
**A. nana* (H. Kraschen.) Muld. China.
**A. nematoloba* (Hand.-Mazz.) Ling & Shih. China.
**A. nitida* Shih. China.
A. nubigena (Wallich) Shih. China.
A. pacifica (Nakai) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum pacificum* Nakai in *Bot. Mag., Tokyo* **42**: 462 (1928) (*Dendranthema pacificum* (Nakai) Kitam.). Japan.
A. pallasiana (Fischer ex Besser) Polj. (*Dendranthema pallasianum* (Fischer ex Besser) Vorosch.). Far East, China, Korea, Japan.
A. parviflora (Grün.) Ling. China.
A. potaninii (H. Kraschen.) Polj. China.
A. przewalskii Polj. China.
**A. purpurea* Shih. China.
**A. remotipinna* (Hand.-Mazz.) Ling & Shih. China.
**A. roborowskii* Muld. China.
A. rupestris (Matsum. ex Koidz.) Muld. Japan.
A. scharnhorstii (Regel & Schmalh.) Tzvelev. C. Asia.
**A. sericea* Shih. China.
A. shiwogiku (Kitam.) Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum shiwogiku* Kitam. in *Acta phytotax. geobot. Kyoto* **4**: 71 (1935). Japan.
A. tenuifolia (Jacquem.) Tzvelev. Himalaya.
A. tibetica (Hook. f. & Thomson) Tzvelev. C. Asia, China, Himalaya.
**A. trilobata* Polj. C. Asia.
**A. tripinnatisecta* Ling & Shih. China.

35. **PHAEOSTIGMA** Muld. in *Bot. Zhurn.* **66**: 586 (1981). Type species: *P. salicifolium* (Mattf.) Muld.

Perennial herbs or half-shrubs. Leaves alternate, pinnatifid to shallowly lobed or entire. Capitula small, densely corymbose,

disciform. Receptacle convex, epaleate. Outer female florets in one row. Central floret corolla 5-lobed; lobes erect. Apical anther appendage subtriangular. Style-branches brownish. Cypselas 4–6-ribbed; ribs projected into minute teeth. Pappus absent.

DISTRIBUTION. China. – 3 spp.

Muldashev made a detailed comparison of *Ajania fruticulosa* and the three species of *Ajania* transferred by him to *Phaeostigma*. According to Muldashev *Phaeostigma* is distinguished by its brownish style-branches and erect corolla lobes. The latter character, as well as the suffruticose habit and the less spiny pollen, are characters similar to those of *Artemisia*. Muldashev stated that phylogenetically *Phaeostigma* is related to the ancestors of *Ajania* and distantly related to *Artemisia*, mainly on account of its pollen morphology.

The brownish style-branches is a difficult character to evaluate. Similar style-branches may be present in related genera. Although Shih & Fu (1983) reduced *Phaeostigma* to synonomy under *Ajania* we have kept them distinct. In that case *Phaeostigma* may be another grade group between *Ajania* and *Artemisia* and its relatives. The actual circumscription of *Phaeostigma* will have to be assessed in a wider study of *Ajania* and especially those *Ajania* species that are similar in habit to *Phaeostigma*.

P. quercifolium (W. Smith) Muld. (*Ajania quercifolia* (W. Smith) Ling & Shih)
P. salicifolium (Mattf.) Muld. (*Ajania salicifolia* (Mattf.) Polj.)
P. variifolium (Chang) Muld. (*Ajania manshurica* Polj., *Ajania ramosa* (Chang) Shih, *Ajania variifolia* (Chang) Tzvelev)

36. **STILPNOLEPIS** H. Kraschen. in *Nov. Sist. Vysshikh Rast.* **2**: 207 (1946). Type species: *S. centiflora* (Maxim.) H. Kraschen. – *Elachanthemum* Ling & Y. R. Ling.

Annual or perennial herbs. Leaves opposite or alternate, pinnatisect, few-lobed or entire. Capitula laxly corymbose, discoid. Involucral bracts widely obovate and largely scarious. Receptacle convex-subconical, epaleate. Corolla 5-lobed, with a distinct tube and more or less crateriform limb, glandular. Apical anther appendage acuminate-triangular. Cypselas obliquely obovoid to narrowly obovoid-oblanceolate, thin-walled, without ribs, densely glandular. Pappus absent.

DISTRIBUTION. Mongolia and China. – 2 spp.

According to Krascheninnikov (1946) *S. centiflora* resembles *Artemisia*, but does not share the obovoid cypselas, the slender corollas, the acuminate anther appendages and the paniculate inflorescence of *Artemisia* and closely related genera. Though elongated, the cypselas are basically the same as in other genera of subtribe Artemisiinae; obovoid (oblanceolate), thin-walled and devoid of ribs. There is no doubt about the subtribal position of *Stilpnolepis*.

According to Ling & Y. R. Ling (1978) the second species, *S. intricata*, formerly classified in *Artemisia* or *Seriphidium*, should be separated from those genera because of the long peduncles and the laxly corymbose inflorescence, the centrally abortive disc florets, and the multicostate appearance of the rows of myxogenic cells on the cypselas. Hence they created a new genus *Elachanthemum* for this species. However, Ling and Y. R. Ling did not consider a possible relationship with *Stilpnolepis*. Recently Shih (1985) argued that *Elachanthemum intricatum* is closely related to *Stilpnolepis centiflora* and his treatment is followed here. Both species have discoid and laxly corymbose capitula, most parsimoniously interpreted as apomorphic within the *Artemisia* group, and hence synapomorphies uniting the two species.

S. centiflora (Maxim.) H. Kraschen.
S. intricata (Franchet) Shih (*Elachanthemum intricatum* (Franchet) Ling & Y. R. Ling

37. **AJANIOPSIS** Shih in *Acta phytotax. sin.* **16**: 86 (1978). Type species: *A. penicilliformis* Shih.

A pubescent annual herb. Leaves alternate, pinnatisect and few-lobed. Capitula rather small, few together in dense corymbs, disciform. Receptacle convex, epaleate. Outer female florets in one row, tapering above, apically densely pilose with erect, straight hairs. Central floret corolla 5-lobed, apically densely pilose with erect, straight hairs. Apical anther appendage subtriangular. Cypselas obovoid, thin-walled with 3–6 rows of myxogenic cells. Pappus absent.

DISTRIBUTION. China, Tibet. – Monotypic.

This is a distinctive species and undoubtedly a member of Artemisiinae, though its immediate relatives are difficult to indicate. Shih (1978) compared it to both *Ajania* and *Artemisia*. It is distinguished by its annual habit, the densely corymbose capitula and apically pilose corollas. The genus differs from *Ajania* only by the corollas being pilose at the apex. The cypsela ribs, described and illustrated by Shih, appear to be rows of myxogenic cells. We have only examined the holotype and avoided consuming type material for a detailed cypsela investigation.

38. **FILIFOLIUM** Kitam. in *Acta phytotax. geobot. Kyoto* **9**: 157 (1940). Type species: *F. sibiricum* (L.) Kitam.

A perennial herb, basally somewhat woody and covered with fibrous leaf sheaths. Leaves alternate, pinnatisect with long filiform lobes. Capitula rather small, corymbose, disciform. Receptacle conical, epaleate. Outer female florets tapering above, minutely 4-dentate. Central florets apparently hermaphrodite but functionally male and female-sterile; corollas compressed together in a resinous mass, 5-lobed. Apical anther appendage triangular. Cypselas obliquely obovoid, thin-walled, with 2 adaxial-lateral rows of myxogenic cells. Pappus absent.

DISTRIBUTION. Far East, China and Korea. – Monotypic.

Filifolium was earlier included in *Artemisia* sect. *Dracunculus* on account of the female-sterile disc florets. However, the inflorescence is corymbose, the style is distinctly divided and the apical appendages of the anthers are triangular, not linear-lanceolate. In habit *Filifolium* is more similar to some species of *Ajania* than to *Artemisia*. In pollen and cypsela characters *Filifolium* is apomorphic compared to *Ajania*. Hence, it occupies an intermediate position within the subtribe, as expressed in the cladogram. The obliquely obovoid cypselas with two distinct rows of myxogenic cells appear to be autapomorphic for this genus.

39. **SPHAEROMERIA** Nutt. in *Trans. Am. phil. Soc.* **2** (7): 401 (1841). Type species: *S. capitata* Nutt. – *Chamartemisia* Rydb. – *Vesicarpa* Rydb.

Perennial herbs or half-shrubs, sometimes rather compact and basally woody. Leaves alternate to rosulate, pinnatisect and few-lobed or entire. Capitula apparently corymbose but sometimes somewhat paniculate or capitate or solitary, disciform. Receptacle flat to conical, epaleate, rarely pubescent. Outer female florets tapering above, sometimes glandular, rarely with dolabriform hairs at the apex. Central florets with corolla 5-lobed, sometimes glandular, rarely with dolabriform hairs at the apex. Apical anther appendage subtriangular. Cypselas obovoid-oblong, sometimes faintly ribbed, sometimes with myxogenic cells, often with an apical rim. Pappus usually absent or rarely minutely coroniform, with small scales.

DISTRIBUTION. Western N. America in California, Colorado, Montana, Nevada, Oregon, Utah and Wyoming, and in Mexico. – 9 spp.

Sphaeromeria was originally proposed by Nuttall to circumscribe *S. capitata* and *S. argentea*. Torrey & Gray (1843) reduced *Sphaeromeria* to a section of *Tanacetum* simply on combination of three plesiomorphic characters, the yellow 5-lobed corollas, the woody base and the alternate leaves. Rydberg (1916) returned *Sphaeromeria* to its generic status and erected two new genera, *Vesicarpa* to include *Artemisia potentilloides* A. Gray with a hairy receptacle and *Chamartemisia* for *Tanacetum compactum* Hall with pappose cypselas.

A. Holmgren et al. (1976) presented a detailed study of the three genera *Sphaeromeria*, *Vesicarpa* and *Chamartemisia*, and concluded that they are more closely related to one another than to any other group. *Sphaeromeria* appears to be more closely related to *Artemisia* than *Tanacetum*. However, of the 12 characters discussed by A. Holmgren et al. not one is autapomorphic for *Sphaeromeria*. They are present in all other genera of Artemisiinae. The presence of a small coroniform pappus in one species is an unusual feature within Artemisiinae but a parallel case is *Crossostephium*.

Sphaeromeria is similar in habit to *Kaschgaria*. The inflorescences of *Sphaeromeria* are variable and the transformations within the genus are difficult to assess. In the cladogram the corymbose condition is considered plesiomorphic but there are species with slightly elongated inflorescences resembling those of *Kaschgaria*. The two genera are possibly closely related.

The list of species is taken from A. Holmgren et al., who also provided a key.

S. argentea Nutt.
S. cana (D. C. Eaton) A. A. Heller
S. capitata Nutt.
S. compacta (H. M. Hall) A. Holmgren, Shultz & Lowrey (*Chamartemisia compacta* (H. M. Hall) Rydb.)
S. diversifolia (D. C. Eaton) Rydb.
**S. martirensis* (Wiggins) A. Holmgren, Shultz & Lowrey
S. potentilloides (A. Gray) A. A. Heller (*Vesicarpa potentilloides* (A. Gray) Rydb.)
S. ruthiae A. Holmgren, Shultz & Lowrey
S. simplex (Nelson) A. A. Heller

40. **KASCHGARIA** Polj. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **18:** 282 (1957). Type species: *K. brachanthemoides* (Winkler) Polj.

Rather woody half-shrubs; indumentum of stellate hairs. Leaves alternate, entire or few-lobed. Capitula rather small and few in an elongated panicle, at the summit fasciculate, disciform. Receptacle conical, epaleate. Outer female florets few, tapering above. Central floret corolla apically with stellate hairs, 5-lobed. Apical anther appendage linear-lanceolate. Cypselas obovoid, thin-walled. Pappus absent.

DISTRIBUTION. C. Asia and China. – 2 spp.

Poljakov removed the two species of *Kaschgaria* from *Artemisia* mainly because of their stellate corolla hairs. He also stated that *Kaschgaria* is closer to *Seriphidium* than to *Artemisia* s. s., but *Kaschgaria* differs from *Seriphidium*, for example, by its disciform (heterogamous) versus a discoid (homogamous) capitulum. The possible relationship to *Sphaeromeria* (then part of *Tanacetum*) was not mentioned by Poljakov, who probably did not consider the North American species of *Tanacetum*. He closed his discussion noting that the systematic position of *Kaschgaria* could not be settled before the whole Asian part of the *Artemisia* group had been properly considered. We agree that *Kaschgaria* is a distinct genus probably related to *Seriphidium*, or possibly more closely to *Sphaeromeria*, although there is no obvious synapomorphy uniting the two genera.

K. brachanthemoides (Winkler) Polj.
K. komarovii (H. Kraschen & N. Rubtzov) Polj.

41. **SERIPHIDIUM** (Besser ex Hook.) Fourr. in *Annls. Soc. linn. Lyon.* II, **17**: 89 (1869) Type species: *S. maritimum* (L.) Polj. – *Artemisia* sect. *Seriphidium* Besser – *Artemisiastrum* Rydb.

Perennial herbs, half-shrubs or annual herbs. Leaves alternate, pinnatisect. Capitula small and few-flowered, oblong, numerous in a long panicle, discoid. Involucral bracts in 4–7 rows, unequal; the outer short and rounded, the inner gradually longer and linear. Receptacle small, conical, epaleate or occasionally paleate. Corolla 5-lobed, tubular, yellow to purple. Apical anther appendage linear-lanceolate. Cypselas small, obovoid to ellipsoid, somewhat flattened or triquetrous, thin-walled. Pappus absent.

DISTRIBUTION. From Europe throughout temperate Asia to N. America (5 spp.), though mainly in central Asia. – 134 spp.

Seriphidium, established as a genus by Poljakov (1961), is almost always considered a section or subgenus of *Artemisia* (e.g. Ward, 1940). We agree with Poljakov (1961), Leonova (1970) and Filatova (1981, 1982*a*, *b* 1984) that it should be kept distinct. *Seriphidium* differs in a number of characters, representing synapomorphies. Furthermore, its sister group appears to be found outside *Artemisia* s. s., and *Seriphidium* cannot be considered a specialized segregate of *Artemisia*. *Seriphidium* is most closely related either to a larger group of genera including *Artemisia* or some other genus (or genera), e.g. *Kaschgaria*, within the Artemisiinae. The genus is characterized by its discoid, homogamous capitula, not disciform and heterogamous as in *Artemisia*. The most parsimonious interpretation for this character is to assume that the outer

female florets present in related genera have been lost. This was originally suggested by Krascheninnikov (1946) although hotly contested by Poljakov (1961). It must be noted that this character breaks down in *S. bigelowii*. This species is usually included in *Artemisia* section *Abrotanum* because there are at least some capitula within inflorescences that have one or two female outer florets. However, on the basis of involucral (many-rowed bracts) and anther (slender apical appendages) characters *S. bigelowii* is certainly a member of *Seriphidium*. It is also virtually identical to the American *S. tridentatum*, which is homogamous and always included in *Seriphidium* (see Weber, 1984). Heterogamy in *S. bigelowii* is plesiomorphic or a secondary reversal from the homogamous condition, which then can be interpreted as a synapomorphy for the genus.

The corollas of *Seriphidium* are tubular and the teeth usually infolded for much of anthesis. During anthesis the short flat lobes of the style are often still together and enclosed in the anther tube, a feature mostly associated with cleistogamy. Mature cypselas are hard to find and there are many occasions when only one will mature in a head of 3–10 florets.

The apical anther appendages of *Seriphidium* are very slender, narrowly lanceolate to linear and notably different from those of *Artemisia* and related genera. The involucre is specialized with 4–7 rows of overlapping bracts, as compared to the 2–4-rowed involucre of related genera.

The monotypic *Artemisiastrum* (*A. palmeri*=*S. palmeri*) was separated by Rydberg (1916) on the presence of receptacular scales. Parallel cases are legion in the Anthemideae and in Asteraceae as a whole. Here the presence of paleae is best considered a gain character, a feature also noted by Hall & Clements (1923). In all characters *S. palmeri* is virtually identical to other taxa within *Seriphidium*.

The list of species has been compiled from the standard floras, cf. under *Artemisia*, and by original research with Y. R. Ling (1991*a*, *b*) during his sabbatical year at The Natural History Museum, London. Except for cases of basionyms, synonymous *Artemisia* names are not included when the same epithet is involved. Also, combinations from *Artemisia* by Bremer & Humphries have been validly published in Ling (1991*a*).

S. algeriense (Filat.) Y. R. Ling. Algeria.
**S. amoenum* (Polj.) Polj. C. Asia.
S. aralense (H. Kraschen.) Polj. SW C. Asia.
S. arbusculum (Nutt.) W. A. Weber. W. United States.
S. arenicolum (H. Kraschen. ex Polj.) Y. R. Ling. Afghanistan, Iran, C. Asia.
***S. argilosum** (Beetle) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia argilosa* Beetle, *Rhodora* **61:** 84 (1959). United States in Colorado.
**S. assurgens* (Filat.) Bremer & Humphries in Y. R. Ling. Russia.
**S. aucheri* (Boiss.) Ling & Y. R. Ling. Iran, Afghanistan, China.
S. badhysi (Krasch. & Lincz. ex Polj.) Polj. C. Asia.
S. balchanorum (H. Kraschen.) Polj. SW C. Asia.
**S. baldshuanicum* (H. Kraschen. & Zaprj.) Polj. Afghanistan, C. Asia.
S. barrelieri (Besser) Soják. Spain, N. Africa.
S. bicolor (Rech. f. & Wagenitz) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia bicolor* Rech. f. & Wagenitz in *Anz. öst. Akad. Wiss. Mathematische Naturwissenschaftliche Klasse.*, **98**: 78 (1961). Afghanistan.
S. bigelowii (A. Gray) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia bigelowii* A. Gray in *Torrey Pacific R. Rep.* **4**: 110 (1857). S. and W. United States.
**S. borotalense* (Polj.) Ling & Y. R. Ling. C. Asia, China.
S. botschantzevii (Filat.) Y. R. Ling. Russia.
**S. brevifolium* (Wallich ex DC.) Ling & Y. R. Ling. Afghanistan, Pakistan, India, China.
S. caerulescens (L.) Soják. S. Europe.
**S. camelorum* (H. Kraschen.) Polj. C. Asia.
S. canum (Pursh) W. A. Weber. W. North America.
S. chitralense (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia chitralensis* Podl., *Fl. iranica* **158:** 198 (1986). Afghanistan, Pakistan.
**S. ciniforme* (H. Kraschen. & Popov ex Polj.) Polj. Iran, C. Asia.
S. cinum (P. Bergius ex Polj.) Polj. C. Asia, China.
S. compactum (Fischer ex DC.) Polj. C. Asia, S. Siberia, China in Sinkiang, Mongolia.
***S. cretaceum** (Fiori) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia caerulescens* var. *cretacea* Fiori in Fiori & Paoletti, *Fl. Italia* **3:** 251 (1904). S. Europe in Italy.
S. densifolium (Filat.) Y. R. Ling. Algeria
S. deserti (H. Kraschen.) Polj. Afghanistan, Iran, SW C. Asia.
S. diffusum (H. Kraschen. ex Polj.) Y. R. Ling. Iran, Afghanistan, Pakistan.
**S. dubjanskyanum* (H. Kraschen. ex Polj.) Polj. C. Asia.
S. dumosum (Polj.) Polj. C. Asia.
**S. dzevanovskyi* (Leonova) Soják. Krym.
**S. elongatum* (Filat. & Ladyg.) Bremer & Humphries in Y. R. Ling. C. Asia.
**S. eremophilum* (H. Kraschen. & Butkov ex Polj.) Bremer & Humphries in Y. R. Ling. C. Asia.
S. federovii (Rzazade) Y. R. Ling. C. Asia.
**S. fedtschenkoanum* (H. Kraschen.) Polj. C. Asia, China in Xinjiang.
**S. ferganense* (H. Kraschen. ex Polj.) Polj. C. Asia.
**S. finitum* (Kitagawa) Ling & Y. R. Ling. China.
S. fragrans (Willd.) Polj. Afghanistan, Caucasus, Iran, C. Asia.
S. freitagii (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia freitagii* Podl., *Fl. iranica* **158**: 193 (1986). Afghanistan.
**S. fulvellum* (Filat. & Ladyg.) Bremer & Humphries in Y. R. Ling. C. Asia.
S. ghazniense (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia ghazniensis* Podl., *Fl. iranica* **158**: 213 (1986). Afghanistan.
S. ghoratense (Podl.) Bremer & Humphries, **comb. nov.** Basionym: *Artemisia ghoratensis* Podl., *Fl. iranica* **158**: 197. Afghanistan.
**S. glanduligerum* (H. Kraschen. ex Polj.) Polj. Afghanistan, Pakistan, C. Asia.
**S. glaucinum* (H. Kraschen. ex Polj.) Bremer & Humphries in Y. R. Ling. C. Asia.
S. gorjaevii (Polj.) Y. R. Ling. C. Asia.
S. gracilescens (H. Kraschen. & Iljin) Polj. C. Asia, S. Siberia, Mongolia, China.
S. grenardii (Franchet) Y. R. Ling & Humphries. China.
**S. gurganicum* (H. Kraschen.) Bremer & Humphries in Y. R. Ling. C. Asia.
**S. gypsaceum* (H. Kraschen., Popov & Lincz. ex Polj.) Polj. Iran, SW & C. Asia.

*S. *halophilum* (H. Kraschen.) Polj. C. Asia.
*S. *heptapotamicum* (Polj.) Ling & Y. R. Ling. C. Asia, China.
S. *herba-album* (Asso) Soják. SW Europe, Turkey, Middle East, Iran, Himalayas.
S. *incultum* (Del.) Y. R. Ling. Egypt.
S. *issykkulense* (Polj.) Polj. C. Asia, China.
S. *junceum* (Karelin & Kir.) Polj. C. Asia, China in Xinjiang.
S. kandaharense (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia kandaharensis* Podl., *Fl. iranica* **158**: 217. Afghanistan.
*S. *karatavicum* (H. Kraschen. & Abolin ex Polj.) Ling & Y. R. Ling. C. Asia, China.
***S. kasakorum** (H. Kraschen.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia maritima* ssp. *kasakorum* H. Kraschen., *Otch. Rab. Pochv.-Bot. Otr. Kazakhst. Exped. Akad. Nauk SSSR* **4**(2): 272 (1930). C. Asia.
*S. *kaschgaricum* (H. Kraschen.) Polj. C. Asia, China in Xinjiang.
*S. *kemrudicum* (H. Kraschen.) Polj. SW & C. Asia.
S. kermanense (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia kermanensis* Podl., *Fl. iranica* **158**: 206 (1986). Iran.
***S. khorassanicum** (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia khorassanica* Podl., *Fl. iranica* **158**: 210 (1986). Iran, Afghanistan.
*S. *knorringianum* (H. Kraschen.) Polj. C. Asia.
*S. *kochiiforme* (H. Kraschen. & Lincz. ex Polj.) Polj. Afghanistan, C. Asia.
*S. *kopetdaghense* (H. Kraschen. ex Polj.) Polj. Afghanistan, Iran, Afghanistan, SW C. Asia.
S. *korovinii* (Polj.) Polj. Afghanistan, C. Asia.
S. *korshinskyi* (H. Kraschen. ex Polj.) Y. R. Ling. Afghanistan.
S. *kurramense* (Qaz.) Y. R. Ling. Afghanistan, Pakistan.
*S. *lehmannianum* (Bunge) Polj. Afghanistan, C. Asia.
S. *lerchianum* (G. Weber in Stechm.) Polj. From SE Europe in Bulgaria through Russia and C. Asia to S. Siberia.
S. *lessingianum* (Besser) Polj. SE Russia, C. Asia, S. Siberia.
S. *leucodes* (Schrenk) Polj. C. Asia.
S. *leucotrichum* (H. Kraschen. ex Polj.) Bremer & Humphries in Y. R. Ling. Afghanistan, Pakistan, C. Asia.
***S. longilobum** (Osterh.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia spiciformis* var. *longiloba* Osterh. in *Muhlenbergia* **4**: 69 (1908). N. America.
S. *maritimum* (L.) Polj. W., N. and E. Europe, Iran, C. Asia and the Himalayas.
S. mendozanum (DC.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia mendozana* DC., *Prodr.* **6**: 105 (1837). W. North America.
*S. *minchunense* Ling & Y. R. Ling. China.
S. *mogoltavicum* (Polj.) Y. R. Ling. C. Asia.
*S. *mongolorum* (H. Kraschen.) Ling & Y. R. Ling. China in Mongolia.
S. *mucronulatum* (Polj.) Y. R. Ling. C. Asia.
*S. *namanganicum* (Polj.) Polj. C. Asia.
*S. *nigricans* (Filat. & Ladyg.) Bremer & Humphries in Y. R. Ling. C. Asia.
*S. *nitrosum* (G. Weber ex Stechm.) Polj. SE Russia, C. Asia, S. Siberia, China in Xinjiang.
*S. *novum* (Nelson) W. A. Weber. W. United States.
S. *nutans* (Willd.) Soják. SE Russia.
*S. *oliverianum* (Gay ex Besser) Bremer & Humphries in Y. R. Ling. Iran, Afghanistan, Pakistan, C. Asia.
S. *oranense* (Deb. ex Filat.) Y. R. Ling. NW Africa (Algeria).
S. *oratense* (Deb. & Filat.) Y. R. Ling. Algeria.
S. palmeri (A. Gray) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia palmeri* A. Gray in *Proc. Am. Acad.* **11:** 79 (1876) (*Artemisiastrum palmeri* (A. Gray) Rydb.). N. America in California and Baja California (Mexico).
S. *pauciflorum* (G. Weber in Stechm.) Polj. SE Russia, C. Asia, S. Siberia.
S. *poljakovii* (Filat.) Y. R. Ling. Russia.
S. *polystichum* (Polj.) Y. R. Ling. C. Asia.
S. *porrectum* (H. Kraschen. ex Polj.) Polj. C. Asia.
*S. *prasinum* (H. Kraschen. ex Polj.) Polj. Afghanistan, C. Asia.
*S. *prolixum* (H. Kraschen. ex Polj.) Polj. C. Asia.
*S. *pygmaeum* (A. Gray) W. A. Weber. W. United States.
***S. quettense** (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia quettensis* Podl., *Fl. iranica* **158**: 212 (1986). Iran, Pakistan.
S. *rhodanthum* (Rupr.) Polj. C. Asia.
*S. *rigidum* (Nutt.) W. A. Weber. W. United States.
S. *rothrockii* (A. Gray) W. A. Weber. W. United States.
S. *saharum* (Pomel) Y. R. Ling. Algeria, Tunisia.
*S. *saissanicum* (H. Kraschen.) Bremer & Humphries in Y. R. Ling. C. Asia.
S. *santolinum* (Schrenk) Polj. (*S. *lobulifolium* (Boiss.) Polj.). Iran, C. Asia.
S. *santonicum* (L.) Soják (*S. *monogynum* (Waldst. & Kit.) Polj.). SE and E. Europe to C. Asia, Turkey.
S. *sawanense* Y. R. Ling & Humphries. China.
S. *schrenkianum* (Ledeb.) Polj. C. Asia, S. Siberia, China in Xinjiang, Mongolia.
*S. *scopiforme* (Ledeb.) Polj. C. Asia, S. Siberia.
*S. *scotinum* (Nevski) Polj. Afghanistan, C. Asia.
*S. *semiaridum* (H. Kraschen. & Lavrenko) Ling & Y. R. Ling. C. Asia.
S. *serotinum* (Bunge) Polj. C. Asia.
*S. *sieberi* (Besser) Bremer & Humphries in Y. R. Ling. Middle East, Iraq, Iran, Afghanistan, SW C. Asia.
S. *skorniakowii* (Winkler) Bremer & Humphries in Y. R. Ling. C. Asia.
*S. *spicigerum* (Koch) Polj. Turkey, Caucasus, Iran.
*S. *stenocephalum* (H. Kraschen. ex Polj.) Polj. Afghanistan, Pakistan, C. Asia.
***S. subchrysolepis** (Filat.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia subchrysolepis* Filat. in *Nov. Sist. Vysshikh Rast.* **18**: 224 (1981). C. Asia.
S. *sublessingianum* (Kell.) Polj. C. Asia, S. Siberia, Mongolia.
*S. *subsalsum* (Filat.) Bremer & Humphries in Y. R. Ling. C. Asia.
S. *szowitzianum* (Besser) Polj. Caucasus.
*S. *tauricum* (Willd.) Polj. Krym, Caucasus, Turkey.
***S. tecti-mundii** (Podl.) Bremer & Humphries, **comb. nov**. Basionym: *Artemisia tecti-mundii* Podl., *Fl. iranica* **158**: 206 (1986). Afghanistan, Pakistan.
S. *tenuisectum* (Nevski) Polj. C. Asia.
S. *terrae-albae* (H. Kraschen.) Polj. C. Asia, Mongolia, China.
*S. *thomsonianum* (C. B. Clarke) Ling & Y. R. Ling. China.
S. *tianshanicum* (H. Kraschen.) Y. R. Ling. C. Asia, China in Xinjiang, Mongolia.
S. *transiliense* (Polj.) Polj. C. Asia.
S. *tridentatum* (Nutt.) W. A. Weber. W. North America.

S. tripartitum (Rydb.) W. A. Weber. W. United States.
**S. turanicum* (H. Kraschen.) Polj. Afghanistan, Iran, Pakistan, C. Asia.
**S. turcomanicum* (Gand.) Polj. Iran, SW & C. Asia.
**S. vachanicum* (H. Kraschen. ex Polj.) Polj. Afghanistan, Pakistan, C. Asia.
**S. validum* (H. Kraschen. ex Polj.) Polj. C. Asia.
S. valesianum (Lam.) Y. R. Ling. C. Europe.
S. vallesiacum (All.) Soják. S. Europe.
**S. vaseyanum* (Rydb.) W. A. Weber. W. United States.

42. **CROSSOSTEPHIUM** Less. in *Linnaea* **6:** 220 (1831). Type species: *C. artemisioides* Less. (*C. chinense* (L.) Makino).

A tomentose shrub. Leaves alternate, narrowly spathulate, apically few-lobed or entire. Capitula rather small and rounded, paniculate, disciform. Outer involucral bracts tomentose, inner scarious. Receptacle hemispherical, epaleate. Outer female florets tubular, 2–3-lobed, glandular. Central florets with corolla tubular, 5-lobed, glandular. Apical anther appendage subtriangular. Cypselas obovoid, weakly 5-ribbed, glandular. Pappus coroniform, of small scales.

DISTRIBUTION. The Philippines, Taiwan, S. Japan, and China, where it is also widely cultivated. – Monotypic.

Crossostephium chinense is a former species of *Artemisia* of uncertain systematic position. The rounded capitula with their pubescent outer involucral bracts recall many species of *Artemisia*. It appears from inflorescence, floret and pollen structure that it is related to the *Artemisia* group of genera. It differs by its weakly ribbed cypselas, furnished with a distinct coroniform pappus. On the basis of these characters a possible relationship to the North American *Artemisia californica* has been suggested by Gray (1884) and Rydberg (1916). Rydberg even transferred some species of *Artemisia* and relatives of *Crossostephium* on the basis of ribbed cypselas being present. However, no pappus is present and the presumed relationship was questioned by Hall & Clements (1923).

43. **ARTEMISIA** L., *Sp. pl.*: 845 (1753). Type species: *A. vulgaris* L. – *Oligosporus* Cass. (including *Artemisiella* A. Ghafoor)

Annual and perennial herbs, half-shrubs or shrubs. Leaves alternate, variously lobed or dissected, rarely entire. Capitula disciform; inflorescence usually a long panicle but sometimes much reduced and racemose, spiciform or subglobose. Receptacle flat to conical, epaleate, sometimes pilose. Outer female florets usually tapering above, with 2–4 teeth, or truncate, commonly oblique at orifice. Central florets hermaphrodite and fertile or female-sterile and functionally male; corolla 5-lobed, yellow or sometimes purplish. Apical anther appendage lanceolate-linear to subulate. Cypselas obovoid, thin-walled, with or without rows of myxogenic cells, usually glabrous but occasionally hairy. Pappus absent.

DISTRIBUTION. Predominantly N. hemisphere but with a few species also from S. America, Africa S. of Sahara and the Hawaiian Islands. Most species in temperate Eurasia and W. N. America. – 388 spp.

Artemisia is the largest genus of the Anthemideae (see Krasheninnikov, 1946). Because there are so many species different authors have made numerous attempts to divide it up in some way. Problems have arisen because two of the four commonly recognized sections appear not to be monophyletic and attempts to separate individual genera have been carried out for a variety of different reasons, in regional isolation, without an appraisal of either all of the characters or all of the taxa.

The division of *Artemisia* goes back to Tournefort (1700). He recognized three genera, *Abrotanum*, *Absinthium*, and *Artemisia*. These were based on gross morphological characters and general habit. They are not the same groups as those recognized today, although the names have been retained at sectional or subgeneric level. Linnaeus (1753) united Tournefort's three genera into one, establishing more or less the concept of *Artemisia* which has been recognized ever since. Cassini (1817) established a new genus, *Oligosporus*, to accommodate those species with functionally separate sexes, outer female florets and central, functionally male florets with fused style-branches and reduced, abortive ovaries. This genus corresponds with the present day section (or subgenus) *Dracunculus*. All of the remaining taxa were included in *Artemisia*, *Absinthium* not being recognized. The next important development was by Besser (1829). Although he never completed his monograph, his results were published by De Candolle (1837). Besser established three subdivisions which were expanded to four by de Candolle as follows:

Sect. *Abrotanum* (=*Artemisia*). Capitula heterogamous (disciform); outer florets female, fertile; central florets perfect, fertile; receptacle glabrous.
Sect. *Absinthium*. As *Abrotanum* but receptacle hairy.
Sect. *Dracunculus*. As *Abrotanum* but central florets female-sterile.
Sect. *Seriphidium*. Capitula homogamous (discoid); florets all perfect, fertile; receptacle glabrous.

This arrangement has more or less persisted ever since and most treatments have fused or separated the different groups. Grenier & Godron (1850) amalgamated all four sections into one genus, *Euartemisia*, but Rouy (1903) by contrast raised three sections, *Seriphidium*, *Abrotanum* and *Absinthium* to the status of subgenera. Later Rydberg (1916) promoted *Dracunculus* to the same rank. Gray (1884) kept sections *Seriphidium* and *Dracunculus* but united *Abrotanum* and *Absinthium* into one new section *Euartemisia*. Hall & Clements (1923) attempted the first phylogenetic interpretation of the four sections, on the basis of three transformations. These were receptacle becoming hairy, loss of female fertility in disc florets and a complete reduction of the female florets. The three sections *Absinthium*, *Dracunculus* and *Seriphidium* were considered to be three coherent groups derived as three separate lines from an ancestral *Abrotanum*.

The most recent treatments have been by Russian and Chinese botanists (Drokhina, 1978; Poljakov, 1961, 1967; Wang, 1979; Leonova, 1971, 1980; Korobkov, 1979). Krascheninnikov (1946) re-sorted Gray's section *Euartemisia*, raising it to subgeneric rank but kept *Dracunculus* and *Seriphidium* as two separate subgenera. The most radical treatment is that of Poljakov (1961). He used the section *Artemisia* s. s. to accommodate distinctive species of the '*Artemisia vulgaris*'-group as distinct from section *Abrotanum*. This, together with sections *Abrotanum* and *Absinthium*, comprised a smaller genus *Artemisia*. *Seriphidium* and *Dracunculus* (=*Oligosporus*) were raised to generic rank

together with some other small genera (*Kaschgaria*, *Neopallasia*, *Turaniphytum* and *Mausolea*).

The most recent classifications of *Artemisia* and its allies are those of Y. R. Ling (1980*b*, 1982, 1984 1988*a*, *b*, 1991*b*). In his 1982 treatment he recognizes nine sections of *Artemisia* and considers *Abrotanum* and *Absinthium* the primitive ones, from where the others, as well as a number of related genera have evolved. It is worth noting that Ling considers *Seriphidium* as a separate genus. Ling (1984) divides the genus into two subgenera, *Artemisia* and *Dracunculus*, and maintains the three traditional sections, *Abrotanum*, *Absinthium* and *Dracunculus*. *Seriphidium* is kept as a separate genus and a number of new combinations are made concerning Chinese species.

Absinthium has been variably maintained as a section, sunk into subgenus *Artemisia* (i. e. *Abrotanum*), or raised to subgeneric rank. The main distinguishing feature, and in fact the only criterion used for recognition, is the presence of a ring of receptacular hairs around the base of each flower. However, even Gray (1884) noted that in certain species there is only a partial presence, or indeed, a complete absence of this character. Poljakov (1961) maintains that it is incorrect to sink *Absinthium* because most species do in fact have the character. He notes also that many species of *Absinthium* have a dense, woolly pubescence of white silky hairs. As far as we can judge, certain species of different sections are artificially separated by this character. Furthermore, there are those taxa with a dense indumentum but without receptacular hairs, and there are those without a silky indumentum but with receptacular hairs. The problem is left to an internal generic study beyond the scope of this work.

The section or subgenus *Dracunculus* is distinguished by the fact that the pistil of the central florets is abortive and they are therefore functionally male. The central ovaries are uniformly sterile and very reduced. This condition is found also in *Mausolea* and *Picrothamnus*. We agree with Hall & Clements (1923) that *Dracunculus* is a monophyletic group, but only so if *Mausolea* and *Picrothamnus* are included. Future work on generic delimitation of *Artemisia* s. l. will probably result in *Dracunculus* being removed from *Artemisia*. As a separate genus it will be named *Oligosporus*, following Cassini (1817) and Poljakov (1961). (*Dracunculus* Miller applies to plants of Araceae.) The problem of *Mausolea* and *Picrothamnus* and their sister group, *Oligosporus* as a whole or only a part of it, also has to be considered, Many species are involved and several new combinations necessary. For these reasons we have for the time being provisionally retained *Oligosporus* as an infrageneric taxon *Dracunculus* within *Artemisia*.

Seriphidium, commonly treated as a section or subgenus of *Artemisia*, is recognized here as a separate genus, following Poljakov (1961) and Y. R. Ling (1982, 1984).

Neopallasia and *Turaniphytum* are two small generic segregates established by Poljakov (1955, 1961). Apparently they have their sister group(s) within *Artemisia*, paraphyletic as presently circumscribed. A proper generic circumscription of *Artemisia*, considering also these segregate genera as well as *Oligosporus* (*Artemisia* sect. *Dracunculus*), *Picrothamnus* and *Mausolea*, is a major task considering the numerous species involved. Work on this problem has been undertaken by Yeou-Ruenn Ling at The Natural History Museum, London and Institute Sinica, Guangzhou.

The list of species is compiled from the major floras, with recently described species added. From those areas, notably China, without recent floristic accounts the list must naturally be taken as rather preliminary. In those cases where major floras disagree on synonymy, the more recent treatments have generally been followed.

**A. abaensis* Y. R. Ling & S. Y. Zhao. China.
A. abrotanum L. Eurasia, widely cultivated and introduced, also in N. America.
A. absinthium L. Eurasia and N. Africa, widely introduced, also in N. America.
A. abyssinica Schultz-Bip. Saudi Arabia.
A. adamsii Besser. S. Siberia, Mongolia, China.
* *A. afghanica* Rech. f. Afghanistan.
A. afra Jacq. Africa S. of Sahara.
**A. aksaiensis* Y. R. Ling. China.
A. alaskana Rydb. N. America in Alaska.
A. albicerata H. Kraschen. C. Asia.
A. aleutica Hultén. Aleutian Islands.
**A. altaiensis* H. Kraschen. S. Siberia, Mongolia.
**A. amygdalina* Decne. Himalayas.
A. andersiana Podl. Afghanistan.
A. anethifolia G. Weber in Stechm. E. Siberia, Mongolia, China.
A. anethoides Mattf. China.
**A. angustissima* Nakai. China, Japan.
A. annua L. Eurasia, widespread and introduced, also in N. America.
A. anomala S. Moore. China.
**A. aquatica* Lour. China.
A. arborescens L. S. Europe, Turkey, Middle East, N. Africa from Libya to Morocco.
A. arctica Less. Siberia, Japan, W. North America.
**A. arctisibirica* Korobkov. Siberia.
A. argyi A. Léveillé & Vaniot. Far East, Mongolia, China, Korea.
**A. argyrophylla* Ledeb. Mongolia, China.
A. armeniaca Lam. SE European Russia, Turkey, Iran, S. Siberia.
A. aschurbajewii C. Winkler. C. Asia.
A. atlantica Cosson & Durieu. N. Africa in Tunisia, Algeria and Morocco.
A. atrata Lam. C. Europe.
A. atrovirens Hand.-Mazz. China.
A. aucheri Boiss. Iran, Pakistan.
**A. aurata* V. Komarov. Far East, China, Korea.
A. australis Less. Hawaii Islands.
A. austriaca Jacq. E. and E.C. Europe, Turkey, Iran, Afghanistan, C. Asia, W. Siberia, Far East, China.
A. austro-himalayensis (Y. R. Ling & H. S. Puri.) Y. R. Ling & H. S. Puri. N. India.
**A. austro-yunnanensis* Ling & Y. R. Ling. China.
**A. avarica* Minat. Caucasus.
**A. baimaensis* Y. R. Ling & Z. C. Z. Y. Zhuo. China.
**A. banihalensis* Kaul & Bakshi. India.
**A. bargusinensis* Sprengel. E. Russia, Siberia.
**A. bejdemaniae* Leonova. Siberia.
A. biennis Willd. Eurasia, widespread and widely introduced, also in N. America.
**A. blepharolepis* Bunge. Mongolia, China.
A. borealis Pallas – *Note:* The delimitation towards *A. campestris* is unclear. In *Flora europaea* (Tutin et al., 1976) this species is treated as a subspecies of *A. campestris*. N. Europe, Siberia, Mongolia, China, N. America.
A. borealo-siamensis Y. R. Ling. N. Thailand

*A. *brachyloba* Franchet. China.
*A. *brachyphylla* Kitam. China, Korea.
*A. *brevis* Pampan. China.
*A. *burmanica* Pampan. China.
A. *caespitosa* Ledeb. S. Siberia, Mongolia, China.
A. *californica* Less. United States in California and Mexico in Baja California.
*A. *calophylla* Pampan. China.
A. *campbellii* Hook. f. & Thomson. Himalayas, China in Tibet.
A. *campestris* L. – *Note:* See note under *A. borealis*. Widespread in Eurasia, N. America, and N. Africa.
A. *camphorata* Villars. Europe.
A. *canariensis* (Besser) Less. Canary Islands.
*A. *cannabifolia* A. Léveillé. China.
A. *cantabrica* (Lainz) Lainz. SW Europe in Spain.
A. *capillaris* Thunb. Far East, China, Japan, SE Asia in Malaya.
A. *carruthii* Wood. W. United States.
A. *caruifolia* Buch.-Ham. in Roxb. Himalayas.
*A. *cashimirica* Kaul & Bakshi. India.
A. *caucasica* Willd. S. European Russia, Caucasus, Turkey.
A. *chamaemelifolia* Villars. C. and SW Europe, Caucasus, Turkey, Iran.
*A. *chiajeana* Kunze. Iran.
*A. *chiarugii* Pampan. China.
*A. *chienshanica* Ling & W. W. Wang. China.
*A. *chingii* Pampan. China.
A. *chitachensis* Cosson ex Battand. & Trabut. N. Africa.
*A. *chrysolepis* Kitagawa. China.
*A. *conaensis* Ling & Y. R. Ling. China.
*A. *congesta* Kitam. Japan.
A. *copa* Philippi. S. America (Argentina & Chile).
*A. *coracina* W. W. Wang. China.
A. *crithmifolia* L. Europe.
*A. *cuspidata* H. Kraschen. E. Siberia.
*A. *daghestanica* H. Kraschen. & Pors. Caucasus and adjacent parts of Russia (Daghestan).
*A. *dahurica* (Turcz.) Polj. China.
*A. *dalai-lamae* H. Kraschen. China in Tibet.
*A. *demissa* H. Kraschen. C. Asia, China.
*A. *densifolia* Filat. Algeria.
*A. *depauperata* H. Kraschen. Mongolia.
A. *desertorum* Sprengel. Far East, E. Siberia, Mongolia, China.
*A. *dimoana* Popov. SW & C. Asia.
A. *disjuncta* H. Kraschen. Mongolia, China.
*A. *divaricata* (Pampan.) Pampan. Mongolia, China.
*A. *diversa* Diels. China.
*A. *dolichocephala* Pampan. Himalayas.
A. *douglasiana* Besser in Hook. f. W. United States.
*A. *dracunculiformis* H. Kraschen. Arctic Siberia.
A. *dracunculus* L. (*A. glauca* Pallas ex Willd.). Eurasia, widely cultivated and introduced, also in N. America.
A. *dubia* Wallich ex Besser. Himalayas, China.
*A. *dudinensis* V. P. Amel'chenko. Siberia.
*A. *duthreuil-de-rhinsi* H. Kraschen. China in Tibet.
*A. *edgeworthii* Balakr. China.
A. *eldarica* Rzazade. Russia.
*A. *elegantissima* Pampan. W. Himalayas.
A. *emeiensis* (Chang) Y. R. Ling. China.
A. *eriantha* Ten. C. and SW Europe.
*A. *eriocephala* Pampan. W. Himalayas.
A. *eriopoda* Bunge. China.
*A. *erlangshanensis* Ling & Y. R. Ling. China.
*A. *faurieri* Nakai. Korea, Japan.
A. *filifolia* Torrey. W. United States.
A. *filiformilobulata* Y. R. Ling & H. S. Puri. India.
A. *flaccida* Hand.-Mazz. China.
*A. *flahaultii* Emb. & Maire. N. Africa in Morocco.
A. *flava* Jurtzev. Siberia.
*A. *flavifolia* Gilli. Afghanistan.
*A. *forrestii* W. Smith. China.
A. *franserioides* Greene. W. N. America.
A. *freyniana* (Pampan.) H. Kraschen. Far East, Mongolia, China, Korea.
A. *frigida* Willd. SE Russia, C. Asia, Siberia, Mongolia, China, N. America.
*A. *frigidioides* H. C. Fu & Z. Y. Zhu. China.
*A. *fukudo* Makino. Korea, Japan.
*A. *fulgens* Pampan. China.
A. *furcata* M. Bieb. E. Siberia, N. America in Alaska and Canada.
*A. *gabriellae* Braun-Blanquet. SW Europe.
A. *gangsuensis* Ling & Y. R. Ling. China.
A. *genipi* G. Weber in Stechm. C. Europe.
*A. *gilvescens* Miq. China, Japan.
A. *giraldii* Pampan. China.
*A. *glabella* Karelin & Kir. China, C. Asia, W. Siberia, Mongolia.
A. *glacialis* L. C. Europe.
*A. *globosa* H. Kraschen. Mongolia, China.
*A. *globosoides* Ling & Y. R. Ling. China.
A. *globularia* Cham. ex Besser. E. Siberia, N. America in Alaska.
A. *glomerata* Ledeb. Arctic and E. Siberia, Japan, N. America in Alaska and Canada (Yukon).
A. *gmelinii* G. Weber in Stechm. Himalayas, C. Asia, Siberia, Far East, Mongolia, China, Korea, Japan.
A. *gongshanensis* Y. R. Ling & Humphries. China.
*A. *gorgonum* Webb in Hook. Cape Verde Islands.
A. *granatensis* Boiss. SW Europe in Spain.
*A. *graveolens* Minat. Caucasus.
*A. *gyangzeensis* Ling & Y. R. Ling. China.
*A. *gyitangensis* Ling & Y. R. Ling. China.
*A. *haichowensis* Chang. China.
A. *hallaisanensis* Nakai. Korea.
*A. *halodendron* Turcz. ex Besser. E. Siberia, Mongolia, China.
*A. *hancei* (Pampan.) Ling & Y. R. Ling. China, Indo-China.
*A. *haussknechtii* Boiss. Turkey, Iraq, Iran.
A. *hedinii* Ostenf. & Pauls in Hedin. China in Tibet.
*A. *henriettae* H. Kraschen. Arctic Siberia.
*A. *hillebrandii* Skottsb. Hawaii Islands.
*A. *hippolytii* Butkov. Russia.
A. *hispanica* Lam. Spain.
A. *hololeuca* M. Bieb. ex Besser. S. European Russia.
A. *hulteniana* Vorosch. Aleutian Islands.
A. *hultenii* Maksimova. Far East.
A. *idilongensis* Y. R. Ling. China.
*A. *ifranensis* J. Didier. N. Africa in Morocco.
*A. *igniaria* Maxim. China.
*A. *implicata* Leonova. Mongolia.
*A. *imponens* Pampan. China.
A. *incana* (L.) Druce. Turkey, Caucasus and adjacent parts of Russia (Daghestan), Iraq, Iran.
A. *incisa* Pampan. (*A. nuristanica* Kitam.). Himalayas.

A. indica Willd. Himalayas, China, Taiwan, Japan.
A. insipida Villars. C. Europe in France.
A. insulana H. Kraschen. E. Siberia in Bering Island.
A. integrifolia L. Siberia, Far East, Mongolia, China, Korea.
**A. intramongolica* H. C. Fu & Z. Y. Zhu. China.
A. jacutica Drob. E. Siberia.
A. japonica Thunb. Afghanistan, Pakistan, Far East, China, Korea, Japan, Taiwan.
A. javanica Pampan. Indonesia.
**A. jaxatica* Polj. C. Asia.
A. jilongensis Y. R. Ling & Humphries. China.
A. judaica L. Middle East and N. Africa in Egypt, Libya and Algeria.
**A. kabylica* Chabert. N. Africa in Algeria.
**A. kanashiroi* Kitam. N. China.
**A. kangmasensis* Ling & Y. R. Ling. China.
**A. karavajevii* Leonova. Siberia.
A. kauaiensis (Skottsb.) Skottsb. Hawaii Islands.
A. kawakamii Hayata. Taiwan.
A. keiskeana Miq. Far East, China, Korea, Japan.
A. kelleri H. Kraschen. C. Asia.
A. kitadakensis Hara & Kitam. Japan.
**A. klementzae* H. Kraschen. ex Leonova. Mongolia.
A. klotzschiana Besser. N. America in Mexico.
A. koidzumii Nakai. E. Siberia, Far East, Japan.
**A. komarovii* Polj. Far East.
**A. kulbadica* Boiss. & Buhse. Iran, C. Asia.
**A. kumykorum* Minat. Caucasus.
A. kuschakewiczii Winkler. C. Asia.
A. laciniatiformis V. Komarov. E. Siberia, Far East, N. America in Alaska.
A. lactiflora Wallich ex DC. China, Taiwan.
A. lagocephala (Fischer ex Besser) DC. Siberia, Far East, China.
A. lagopus Fischer ex Besser. E. Siberia, Far East.
A. lamprocaulos Rech. f. Iran.
A. lancea Vaniot (*A. feddei* Lévl. & Vaniot). China, Korea, Japan.
A. latifolia Ledeb. Russia, C. Asia, Siberia, Mongolia, China.
A. lavandulifolia DC. Far East, China, Korea.
**A. lavei* Kostel. China.
A. ledebouriana Besser. E. Siberia.
**A. leontopodioides* Fischer ex Besser. E. Siberia, Aleutian Islands.
A. leptophylla D. Don. Himalayas (Nepal).
A. leucophylla (Turcz. ex Besser) C. B. Clarke. S. Siberia, Mongolia, China.
**A. limosa* Koidz. Far East.
**A. limprichtii* (Pampan.) Ling & Y. R. Ling. China.
**A. lipskyi* Polj. C. Asia.
**A. littoricola* Kitam. Far East, Japan.
A. longifolia Nutt. Canada and W. United States.
A. ludoviciana Nutt. Canada and W. United States.
**A. macilenta* (Maxim.) H. Kraschen. Far East, China.
**A. maciravae* Hutch. & Dalziel. Africa in Sahara.
A. macrantha Ledeb. European Russia, Siberia, Mongolia, China.
A. macrocephala Jacq. Iran, Afghanistan, Himalayas, S. Siberia, Far East, Mongolia, China.
**A. macrorhiza* Turcz. E. Siberia.
A. magellanica Schultz-Bip. S. America in Chile.
A. mairei A. Léveillé. China.
**A. manshurica* (V. Komarov) V. Komarov. Siberia, China.
A. maroccana Cosson. Morocco.
**A. marschalliana* Sprengel. China.
**A. martjanovii* H. Kraschen. ex Polj. E. Siberia.
A. mattfeldii Pampan. China.
A. mauiensis (A. Gray) Skottsb. Hawaii Islands.
A. maximovicziana (F. Schum.) H. Kraschen. ex Polj. Far East.
**A. medioxima* H. Kraschen. ex Polj. Far East, N. China.
A. melanolepis Boiss. & Kotschy. Iran.
A. mesatlantica Maire. N. Africa in Morocco.
A. michauxiana Besser. W. North America.
A. minor Jacq. in Besser. Himalayas, China in Tibet.
**A. molinieri* Quezel, Barbero & R. Loisel. SW Europe in France.
**A. molluccana* Roxb. SE Asia in the Moluccas.
A. momiyamae Kitam. Japan.
A. mongolica (Fischer ex Besser) Nakai. China.
A. monophylla Kitam. Japan.
A. monosperma Del. Turkey, Middle East, N. Africa in Egypt and Libya.
A. montana Pampan. Far East, China, Japan.
**A. montevidensis* Sprengel. S. America in Argentina.
**A. moorcroftiana* Wallich ex DC. China.
A. morrisonensis Hayata. Taiwan.
**A. multisecta* Leonova. C. Asia.
A. mutellina Villars. C. & S. Europe.
**A. myriantha* Wallich ex DC. China, Himalyas, Burma.
**A. nakaii* Pampan. China, Korea.
**A. nanshanica* H. Kraschen. China in Tibet.
**A. neglecta* Leonova. C. Asia.
**A. negrei* Ouyahya. Morocco.
**A. nesiotica* Raven. W. United States.
A. niitakayamensis Hayata. Taiwan.
A. nilagirica (C. B. Clarke) Pampan. India, Burma.
A. nitida Bertol. C. Europe.
**A. nivalis* Braun-Blanquet. C. Europe in Switzerland.
**A. nortonii* Pampan. China in Tibet.
A. norvegica Fries. N. Europe, Arctic America.
**A. nujianensis* (Ling & Y. R. Ling) Y. R. Ling. China.
A. obscura Pampan. Mongolia, China.
A. obtusiloba Ledeb. C. Asia, S. Siberia, Mongolia.
**A. occidentali-sichuansensis* Y. R. Ling. China.
A. occidentali-sinensis Y. R. Ling. China.
A. occidentali-yunnanensis Ling & Y. R. Ling. China.
A. oelandica (Besser) V. Komarov. N. Europe in Sweden.
**A. olchonensis* Leonova. Siberia.
**A. olgensis* (Vorobiev) Vorosch. Russia.
A. oligocarpa Hayata. Taiwan.
A. opulenta Pampan. N. Japan, E. Russia.
**A. oranensis* Filat. Algeria.
**A. ordosica* H. Kraschen. China.
**A. orientalis* (Pampan.) Ling & Y. R. Ling. China.
A. orientali-hengduangensis Ling & Y. R. Ling. China.
A. orientali-xizangensis Y. R. Ling & Humphries. China.
A. orientali-yunnanensis Y. R. Ling. China.
**A. orthobotrys* Kitagawa. China.
**A. oxycephala* Kitagawa. China.
**A. packardiae* Grimes & Ertter. W. United States.
**A. pallens* Wallich ex Besser. India.
A. palustris L. S. Siberia, Far East, Mongolia, China. Mongolia, China, Korea.
A. pancicii (Janka) Ronniger. E.C. Europe.
**A. pannosa* H. Kraschen. Far East.
A. papposa Blake & Cronq. W. United States in Idaho.

A. parryi A. Gray. W. United States.
A. parviflora Buch.-Ham. ex Roxb. China.
A. pattersonii A. Gray. W. United States.
**A. pedatifida* Nutt. W. and C. United States.
A. pedunculosa Miq. Japan.
**A. pengchuoensis* Y. R. Ling & S. Y. Zhao. China.
A. persica Boiss. Iran, Afghanistan, Himalayas, C. Asia.
**A. pewzowii* Winkler. China in Tibet.
**A. phaeolepis* H. Kraschen. S. Siberia, Mongolia, China.
**A. phyllobotrys* (Hand.-Mazz.) Ling & Y. R. Ling. China.
**A. polybotryoidea* Y. R. Ling. China.
A. pontica L. C. and E. Europe, W. Siberia, introduced in N. America.
**A. porteri* Cronq. W. United States in Wyoming.
**A. praticola* Klokov. Ukraine.
**A. prattii* (Pampan.) Ling & Y. R. Ling. China.
A. princeps Pampan. China, Korea, Japan, Taiwan.
**A. przewalskii* H. Kraschen. China.
A. pseudopontica Schur. E. Europe.
**A. pubescens* Ledeb. China.
**A. punctigera* H. Kraschen. Far East, European Russia, E. and W. Siberia, Mongolia, N. America.
**A. pycnorhiza* Ledeb. C. Asia, S. Siberia, Mongolia.
**A. quinlingensis* Ling & Y. R. Ling. China.
**A. quinqueloba* Trautv. C. Asia.
**A. ramosa* C. Smith. Canary Islands.
**A. rehan* Chiov. Africa in Ethiopia.
**A. remotiloba* H. Kraschen. ex Polj. E. Siberia.
A. reptans C. Smith ex Link. SW Europe in Spain, N. Africa in Morocco, Canary Islands.
**A. robusta* (Pampan.) Ling & Y. R. Ling. China.
**A. rosthornii* Pampan. China.
A. roxburghiana Besser. Afghansitan, Pakistan, Himalayas, China.
**A. rubripes* Nakai. Far East, Mongolia, China, Korea, Japan.
A. rupestris L. N. Europe, C. Asia, W. Siberia, Mongolia, China, N. America in Canada.
A. rutifolia Stephen ex Sprengel. Iran, Afghanistan, Himalayas, C. Asia, Siberia, Mongolia, China.
A. sacrorum Ledeb. China, Korea, Japan, Himalayas, C. Asia, Afghanistan.
**A. saitoana* Kitam. Far East, Korea.
A. salsoloides Willd. Russia, W. Himalayas, W. Siberia, China in Tibet.
**A. samoiedorum* Pampan. Arctic Siberia.
A. santolinifolia Turcz. ex H. Kraschen. Afghanistan, China in Tibet, European Russia, C. Asia, S. Siberia, Mongolia, Pakistan.
**A. saposhnikovii* H. Kraschen. ex Polj. C. Asia.
A. schimperi Schultz-Bip. ex Schweinf. Africa in Ethiopia.
**A. schischkinii* H. Kraschen. Mongolia.
A. schmidtiana Maxim. Far East, Japan.
A. scoparia Waldst. & Kit. C. and E. Europe, Turkey, Middle East, Iran, Himalayas, C. Asia, Siberia, Mongolia, China, Japan, N. Africa in Egypt.
A. scopulorum A. Gray. W. United States.
A. selengensis Turcz. ex Besser. E. Siberia, Far East, Mongolia, China.
A. senjavinensis Besser. E. Siberia, N. America in Alaska.
A. sericea G. Weber in Stechm. Russia, Siberia, Mongolia, China.
A. serrata Nutt. W. United States.
**A. serreana* Pampan. China.
**A. shangnanensis* Ling & Y. R. Ling. China.
**A. shennongjaensis* Ling & Y. R. Ling. China.
**A. sichuanensis* Ling & Y. R. Ling. China.
A. sieversiana Ehrh. in Willd. European Russia, Himalayas, C. Asia, Siberia, Far East, China.
**A. simulans* Pampan. China.
A. sinanensis Yabe. Japan.
A. sinensis (Pamp.) Ling & Y. R. Ling. China.
A. smithii Mattf. China.
**A. somai* Hayata. Taiwan.
A. songarica Schrenk. C. Asia, China.
**A. speciosa* (Pampan.) Ling & Y. R. Ling. China.
**A. sphaerocephala* H. Kraschen. Mongolia, China.
A. splendens Willd. Turkey, Caucasus, Iraq, Iran.
A. stelleriana Besser. Far East, China, introduced in N. Europe and N. America, Japan.
A. stenophylla Kitam. China, Korea, E. Russia.
A. stipularis Urb. & Ekman. Haiti.
A. stolonifera (Maxim.) V. Komarov. Far East, China, Japan.
A. stracheyi Hook. f. & Thomson ex C. B. Clarke (Note added in proof. This taxon was recently removed by Ghafoor (1992) and described as a monotypic genus under the name *Artemisiella stracheyii* (Hook. f. & Thomson ex C. B. Clarke) Ghafoor). Himalayas, China in Tibet.
A. stricta Edgew. Iran, Himalayas, China in Tibet.
**A. subulata* Nakai. Soviet Far East, China, Korea.
A. subviscosa Turcz. E. Siberia.
**A. succulenta* Ledeb. C. Asia, W. Siberia.
**A. succulentoides* Ling & Y. R. Ling. China.
A. suksdorfii Piper. W. Canada and United States.
**A. superba* Pampan. Mongolia.
A. swatensis Podl. Pakistan.
A. sylvatica Maxim. Far East, Mongolia, N. China.
**A. tafelii* Mattf. China in Tibet.
A. taibaishanensis Y. R. Ling & Humphries. China.
**A. tainingensis* Hand.-Mazz. China.
A. tanacetifolia L. China, N. Korea, C. and W. Russia, Europe, N. America.
A. tangutica Pampan. China.
A. tenuifolia Y. R. Ling & H. S. Puri. China.
A. thellungiana Pampan. SW China, N. India, Sikkim.
A. tilesii Ledeb. Arctic Eurasia and Arctic N. America.
A. tomentella Trautv. C. Asia.
A. tournefortiana Reichenb. Turkey, Caucasus, Iran, Afghanistan, Himalayas, C. Asia, Mongolia, China.
**A. transbaicalensis* Leonova. Siberia.
**A. trautvetteriana* Besser. S. European Russia.
A. tridactyla Hand.-Mazz. China.
**A. triniana* Besser. Arctic Siberia.
A. tschernieviana Besser. E. Europe, C. Asia, China.
**A. tsugitakaensis* (Kitam.) Ling & Y. R. Ling. China.
**A. tsuneoi* Tatewaki & Kitam. Japan.
**A. tukuchaensis* Kitam. Himalayas (Nepal).
A. tyitangensis Ling & Y. R. Ling. China.
A. unalaskensis Rydb. Far East, N. America in Alaska.
**A. ussuriensis* Polj. Far East.
**A. velutina* Pampan. China.
**A. verbenacea* (V. Komarov) Kitagawa. China.
A. verlotorum Lamotte. China, Himalayas, Malaya, naturalized in W. and C. Europe and in N. Africa, S. America.
A. vestita Wallich ex Besser. W. Himalayas.
A. vexans Pampan. China, Himalayas.
**A. viridisquama* Kitam. China.

**A. viridissima* (V. Komarov) Pampan. China.
**A. viscida* (Mattf.) Pampan. Himalayas, China.
**A. viscidissima* Ling & Y. R. Ling. China.
A. vulgaris L. Widespread in Eurasia and N. America, also in N. Africa, widely introduced e. g. in Australia.
**A. waltonii* J. R. Drumm. ex Pampan. China in Tibet.
**A. wellbyi* Hemsley & Pears. China, Himalayas.
**A. wudanica* Liou & W. Wang. China.
**A. xanthochloa* H. Kraschen. Mongolia, China.
**A. xerophytica* H. Kraschen. Mongolia, China.
**A. xigazeensis* Ling & Y. R. Ling. China.
**A. yadongensis* Ling & Y. R. Ling. China.
A. yongii Y. R. Ling. China.
**A. younghusbandii* J. R. Drumm. China in Tibet.
A. yunnanensis Jeffrey ex Diels. China.
**A. zayuensis* Ling & Y. R. Ling. China.
A. zhongdianensis Y. R. Ling. China.

44. **NEOPALLASIA** Polj. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **17**: 429 (1955). Type species: *N. pectinata* (Pallas) Polj.

Annual or biennial herbs. Leaves alternate, pectinate-pinnatisect with filiform, apically somewhat swollen and mucronulate lobes. Capitula rather small and rounded in a narrow spiciform panicle, disciform. Receptacle narrowly conical, epaleate. Outer female florets narrowly tubular, without teeth. Central florets of two kinds; outer perfect, inner completely sterile with reduced ovaries. Apical anther appendage ovoid-lanceolate and acuminate. Cypselas arranged around the base of the receptacle, oblong-obovoid, somewhat compressed or triquetrous, thin-walled, with many rows of myxogenic cells. Pappus absent.

DISTRIBUTION. C. Asia, S. Siberia, Mongolia and China. – 3 spp.

Poljakov (1955) distinguished *Neopallasia* from *Artemisia* by the characteristic pectinate leaves, the apically truncate (without teeth) outer female florets, the presence of completely sterile central florets (in addition to perfect ones) situated at the apex of a narrowly conical receptacle, the ovoid-lanceolate and attenuate anther appendages and the rosette-shaped arrangement of the cypselas around the receptacle. These characters are autapomorphies, though the shape of the anther appendages is hardly spectacular considering the variation present within the subtribe, and the cypsela arrangement follows from the sex distribution within the head, fertile florets being restricted to the outer part or the base of the conical receptacle.

The immediate relatives or the sister group of *Neopallasia* is not easy to identify. Poljakov suggested that the genus is related to *Artemisia* sect. *Dracunculus* because some of the central hermaphrodite florets are sterile. It does seem clear that *Neopallasia* has its sister group within a presently paraphyletic *Artemisia*, possibly within sect. *Dracunculus* as suggested by Poljakov.

Y. R. Ling (1980*a*) has recently added two Chinese species. The material of those were formerly considered part of *N. pectinata* s. l.

N. pectinata (Pallas) Polj.
N. tibetica Y. R. Ling
**N. yunnanensis* (Pampan.) Y. R. Ling

45. **TURANIPHYTUM** Polj. in Komarov, *Fl. URSS* **26:** 880 (1961). Type species: *T. eranthemum* (Bunge) Polj.

Perennial herbs, somewhat woody at the base. Leaves alternate to rosulate, pinnatisect. Capitula disciform; inflorescence a spike of glomerules with densely congested capitula, or rarely capitula solitary in interrupted, partly congested spikes. Receptacle convex to hemispherical, epaleate. Outer female florets subtended by scaphoid inner involucral bracts, unequally crenate at the apex. Central florets 5-lobed, apically with long rigid somewhat reddish hairs at the apex. Apical anther appendage lanceolate, acuminate. Cypselas obliquely oblong-obovoid, thin-walled, with rows of myxogenic cells. Pappus absent.

DISTRIBUTION. C. Asia. – 2 spp.

Turaniphytum was distinguished from *Artemisia* mainly because of the peculiar inflorescence, with the capitula aggregated into glomerules and arranged in long spikes. These are presumably transformed paniculate inflorescences of the common *Artemisia* type. *Turaniphytum* also has scaphoid inner involucral bracts, subtending the outer female florets. The immediate relatives of *Turaniphytum* are unknown. It may have its sister group within *Artemisia*.

T. codringtonii (Rech. f.) Polj. (*T. kopetdaghense* Polj.). Afghanistan.
T. eranthemum (Bunge) Polj.

46. **MAUSOLEA** Polj. in *Trudy Inst. Bot. Alma-Ata* **11:** 170 (1961). Type species: *M. eriocarpa* (Bunge) Polj.

A virgate shrub. Leaves alternate, few-lobed or entire. Capitula small and subglobose, rather few and more or less sessile in a reduced panicle, disciform. Receptacle epaleate. Outer female florets without corolla; style-branches dilated, lanceolate, flat, acute. Central florets 5-lobed, apically with bifurcate hairs, hermaphrodite and female-sterile; ovaries reduced and style-branches fused. Apical anther appendage narrowly lanceolate-linear. Cypselas obovoid, densely pilose. Pappus absent.

DISTRIBUTION. Iran, Afghanistan, and C. Asia. – Monotypic.

Mausolea was separated from *Artemisia* mainly because of the corollaless marginal flowers. The styles of the marginal flowers are also further modified compared to those of *Artemisia*, being wider and lanceolate. It is probably related to *Picrothamnus* as discussed under that genus. The cypsela hairs are straighter and less cobwebby in *Mausolea* compared to *Picrothamnus*.

47. **PICROTHAMNUS** Nutt. in *Trans. Amer. Philippi Soc.* II, **7:** 417 (1841). – Type species: *P. desertorum* Nutt.

A basally much woody shrublet with older branches transformed into long spines. Leaves alternate, few-lobed. Capitula small and subglobose, solitary or few together along the branches, almost sessile, disciform. Receptacle epaleate. Outer female florets tubular. Central florets 5-lobed, with long cobwebby bifurcate hairs, hermaphrodite and female-sterile; ovary reduced and style-branches fused. Apical

anther appendage lanceolate-linear. Cypselas obovoid, thin-walled, densely cobwebby-pilose with bifurcate hairs. Pappus absent.

DISTRIBUTION. N. America in western United States. – Monotypic.

Picrothamnus was established by Nuttall but reduced by Eaton (in Watson, 1871), a classification accepted by most later authors. Hence it is generally known as *Artemisia spinescens* D. C. Eaton. Hall & Clements (1923) consider it 'in all essentials an *Artemisia* of the section *Dracunculus*'. The spiny habit and the cobwebby-pilose corollas are autapomorphies of *Picrothamnus*. The cobwebby-pilose cypselas are shared with *Mausolea*, the probable sister group. Together they are related to *Artemisia* sect. *Dracunculus* because of their functionally male central florets with reduced ovaries and fused style-branches. Pending a revised generic delimitation of *Artemisia* we think these genera should be retained rather than sunk in *Artemisia*.

7. **ACHILLEINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Achillea millefolium* L.

Herbae annuae vel perennes vel suffrutices. Receptaculum paleaceum. Corolla flosculorum disci tubo varie saccato et incrassato, saltem adaxialiter basi saccato. Cypselae parietibus tenuibus, plerumquefasciculis vascularibus duobus lateralibus interdum etiam fasciculo uno adaxiali vel nonnunquam fasciculis 4–5 instructae, interdum compressae, saepe cellulis mucilaginis instructae. Pappus nullus.

Annual or perennial herbs or shrublets. Leaves variously dissected, sometimes vermiform, rarely few-lobed or entire. Capitula solitary or corymbose, radiate or discoid. Receptacle variously shaped, often conical, paleate. Ray floret limb white or yellow. Disc corolla 5-lobed; tube variously saccate and thickened in fruit, basally saccate at least adaxially. Cypselas thin-walled, generally with 2 lateral and with or without 1 adaxial strand, sometimes 4–5-stranded, sometimes flattened, often with myxogenic cells. Pappus absent.

DISTRIBUTION (Table 16): Eurasia and N. Africa, mainly in S. Europe, the Mediterranean and SW Asia, also in N. America, some species of *Achillea* widely introduced also in the S. hemisphere and one species of *Santolina* introduced in N. America. – 9 genera, 147 spp.

Some groupings within this subtribe have been recognized earlier. The relationship between *Achillea*, *Anacyclus*, and *Leucocyclus* has been pointed out by Humphries (1979) and phytochemical investigations have indicated a close relationship between *Chamaemelum* and *Cladanthus*. Both genera accumulate similar thiophene derivatives (Greger, 1977). Phytochemistry has also contributed to the recognition of subtribe Achilleinae. *Achillea* and *Anacyclus*, *Chamaemelum* and *Cladanthus*, as well as *Otanthus*, all synthesize amides (Greger, 1977; Bohlmann et al., 1973). *Santolina* has a different chemistry, plesiomorphic in being similar to *Tanacetum*, but it is here provisionally accepted in Achilleinae because of its adaxially saccate corolla and the paleate receptacle. *Leucocyclus*, *Mecomischus*, and *Rhetinolepis*, three little-known North African genera, are also included in Achilleinae and considered related to *Chamaemelum* and *Cladanthus* on a number of morphological characters. *Mecomischus* and *Rhetinolepis* have not been investigated chemically.

The cladogram is one of nine equally parsimonious cladograms. They involve rearrangements at the base and among the last four genera. In all cladograms and hence also in the strict consensus tree, clades Ac4 (*Achillea*, *Anacyclus*, *Leucocyclus*), Ac5 (*Anacyclus* and *Leucocyclus*), Ac6 (*Mecomischus*, *Chamaemelum*, *Rhetinolepis*, *Cladanthus*), and Ac8 (*Rhetinolepis* and *Cladanthus*) were present.

Clades and characters – Fig. 8, Tables 2, 17.

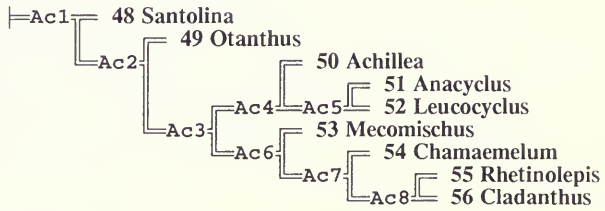

Fig. 8 Cladogram (of nine possible) of the Achilleinae produced by the *ie* option. Cladogram length = 34, consistency index = 88, retention index = 85.

Clade Ac1 – subtribe Achilleinae

45 *Receptacle paleate.*

82 *Disc corolla tube thickened in fruit.* This character is variously strongly expressed in the different genera, most clearly in *Otanthus*. It is hardly evident in *Achillea*, *Anacyclus*, and *Leucocyclus*.

Table 16 General distribution of Achilleinae and genera. x=indigenous, o=introduced.

	N.Am.	Eur-Asia	C.& E. Asia	SW Asia	S.Eur.	N.Afr.	S.Afr.	Austr. N.Zeal.	S.Am.
Achilleinae	o	x	x	x	x	x	o	o	o
Santolina	o				x	x			
Otanthus		x	x	x					
Achillea	o	x	x	x	x	x	o	o	o
Anacyclus		x			x	x			
Leucocyclus		x							
Mecomischus						x			
Chamaemelum		x			x	x			
Rhetinolepis						x			
Cladanthus					x	x			

Table 17 Data matrix for the Achilleinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 1 1 1 111 111 1 14505765 4887 38 28351116284358 351471 53271811 52422519960847917519401740 1836
48. *Santolina*	a1?a111a a1111100000000000p000000000p000
49. *Otanthus*	01?a1?1a a1110111110000000000000000000000
50. *Achillea*	a1aa111a a0110p10p011100p0000000000p000
51. *Anacyclus*	a1aa1?1a a0110p100011111a000000p0000000
52. *Leucocyclus*	a1aa1?10 a01100?000111110110000000000000
53. *Mecomischus*	a1aa1?1a a11100?00010000000a11?p0000000
54. *Chamaemelum*	a1aa111a a1110p100010000000a111p0000000
55. *Rhetinolepis*	a1?a1?1a a11101?000100000000117?11111000
56. *Cladanthus*	a10a1?1a a1110010001000000011111111010111

	1111 11 1 167772555566666617 141383 360561356790567851324 6726
48. *Santolina*	??????????????????0p00000
49. *Otanthus*	??????????????????0000000
50. *Achillea*	???000000000000000000pppp0
51. *Anacyclus*	???000000000000000000p0000
52. *Leucocyclus*	?????000000000000000000000
53. *Mecomischus*	?????000000000000000000000
54. *Chamaemelum*	???000000000000000000000p
55. *Rhetinolepis*	??????????????????000000
56. *Cladanthus*	???000000000000000000000

84 *Disc corolla tube basally saccate at least adaxially.*

172 *Pappus absent in ray and disc cypselas.*

Santolina

2 *Plants shrubby.*

35 *Capitula discoid.* Some *Anacyclus* and *Chamaemelum* species are also discoid, as well as *Otanthus* and *Rhetinolepis*.

Clade Ac2

181 *Amides present. Leucocyclus*, *Mecomischus*, and *Rhetinolepis* have not been investigated chemically.

Otanthus

9 *Plants covered with a dense greyish-white indumentum.*

15 reversed. *Leaves not variously deeply lobed or divided, but entire or crenulate only.*

29 *Capitula densely corymbose.* Most species of *Achillea* also have densely corymbose capitula.

35 *Capitula discoid.*

86 *Corolla basally copiously swollen and spongy, almost enclosing the cypsela especially laterally.*

Clade Ac3

130 *Cypselas with 2 lateral vascular strands, sometimes also with 1 adaxial strand.* This cypsela vascularization is also characteristic of a large part of subtribe Matricariinae, but the two groups do not seem closely related.

Clade Ac4

58 *Ray and disc floret tube dorsiventrally flattened.*

82 reversed. See clade Ac1.

114 *Cypselas dorsiventrally flattened.* Flattened cypselas occur in various subtribes.

Achillea

There is no obvious autapomorphy for this large genus.

Clade Ac5

117 *Cypselas laterally winged.* Some genera of the *Cotula* group (Matricariinae) also have winged cypselas. As noted above (clade Ac3) the groups are not closely related.

119 *Cypselas with sclerenchymatic lateral wings.*

Anacyclus

61 *Ray floret tube persistent on the cypsela.* This character occurs also in some genera of subtribe Thaminophyllinae.

Leucocyclus

27 *Leaves vermiform.* Some species of *Santolina* also have vermiform leaves.

51 reversed. *Floral parts without resin canals.*

85 *Disc corolla deeply and equally saccate both abaxially and adaxially.*

Clade Ac6

41 *Involucral bracts wide, flabelliform.* This character reverses in the small-headed genus *Rhetinolepis*.

139 *Cypselas completely covered with rows of myxogenic cells.*

154 *Cypselas thin-walled, obovoid to oblanceolate, devoid of ribs.* The same type of cypselas is characteristic of the unrelated *Artemisia* and allies in subtribe Artemisiinae.

Mecomischus

There is no obvious autapomorphy for this little-known genus.

Clade Ac7

180 *Particular thiophene derivatives present. Rhetinolepis* has not been investigated chemically.

Chamaemelum

There is no autapomorphy for *Chamaemelum*. The genus is variable in several characters.

Clade Ac8

1 *Plants annual.* Some species of *Chamaemelum* and other genera of the Achilleinae are also annuals.

7 *Plants with branches in whorls below the first capitula.* The capitula of *Rhetinolepis* and *Cladanthus* are very different in size and shape, but sessile (following character) and arranged similarly.

34 *Capitula sessile along the stems.*

50 *Receptacular paleae pilose.* This character also occurs in some species of *Chamaemelum*, as well as in the unrelated *Eriocephalus* in subtribe Matricariinae.

Rhetinolepis

11 *Plants with dolabriform hairs.*

35 *Capitula discoid.*

41 reversed. See clade Ac6.

Cladanthus

48 *Receptacle pilose.* Some genera of subtribe Thaminophyllinae also have pilose receptacles.

52 reversed. *Ray floret limb not white, but yellow.*

73 *Disc corolla lobes with dorsal appendages.* Corolla lobe appendages occur also in various genera of subtribes Leucantheminae and Matricariinae.

116 *Disc cypselas laterally flattened.* Laterally flattened but otherwise quite different cypselas occur in subtribe Chrysantheminae.

48. **SANTOLINA** L., *Sp. pl.*: 842 (1753). Type species: *S. chamaecyparissus* L.

Shrublets. Leaves alternate, dentate to pinnatifid or pinnatisect, sometimes vermiform. Capitula solitary, pedunculate, discoid. Receptacle convex, paleate; paleae with a central resin canal. Corolla 5-lobed, basally saccate around the cypsela especially adaxially, with a rather long bent tube and a distinct limb. Cypselas 3–5-angled, sometimes with myxogenic cells. Pappus absent.

DISTRIBUTION. S. Europe, mainly in Spain but extending to Jugoslavia, and N. Africa in Morocco and Algeria, one species (*S. rosmarinifolia*) introduced in N. America. – 8 spp.

Santolina is provisionally placed in Achilleinae. It differs in chemistry from the other genera of this subtribe, containing polyacetylenes and other substances similar to those in *Tanacetum* (Greger, 1977). It may be a derivative of that genus rather than the sister group of the genera of Achilleinae. Although some efforts have already been made to identify taxa based on chromosome numbers (e.g. Arrigoni, 1977) *Santolina* is in need of revision. There are two species, *S. chamaecyparissus* and *S. rosmarinifolia*, with numerous synonyms and many variants. A few 'species' have been described from North Africa. Apparently they belong under the complex European species.

S. chamaecyparissus L.
S. elegans Boiss. ex DC.
**S. insularis* (Gennari ex Fiori) Arrig.
**S. ligustica* Arrig.
**S. marchi* Arrig.
S. oblongifolia Boiss.
S. rosmarinifolia L.
S. viscosa Lagasca

49. **OTANTHUS** Hoffsgg & Link, *Fl. portug.* **2**: 364 (1889). Type species: *O. maritimus* (L.) Hoffsgg & Link – *Diotis* Desf.

A suffruticose perennial covered with a dense greyish-white indumentum. Leaves alternate, entire or crenulate. Capitula corymbose, discoid. Receptacle convex, paleate; paleae with a central resin canal. Corolla 5-lobed, basally copiously swollen and spongy, almost enclosing the cypsela especially laterally. Cypselas with 4–5 weak ribs, thin-walled, glandular. Pappus absent. Amides present.

DISTRIBUTION. Europe, N. Africa, and SW Asia extending from Ireland to Caucasus, along sea shores, mainly in the Mediterranean. – Monotypic.

This characteristic species is known also as *Diotis candidissima* Desf. The interrelationships of *Otanthus* have been obscure but it seems that it is an autapomorphic member of subtribe Achilleinae, sharing the same chemistry as most members of the subtribe. The copiously swollen corolla base also indicates the same relationship, though the character is not so extremely developed in the other genera.

50. **ACHILLEA** L., *Sp. pl.*: 896 (1753). Type species: *A. millefolium* L.

Perennial herbs generally with rhizomes. Leaves alternate, pinnatisect, lobed or rarely entire. Capitula comparatively small, generally corymbose or rarely few together or solitary, radiate or rarely discoid. Receptacle flat to convex or conical or rarely much elongated, paleate; paleae sometimes with a central resin canal. Ray florets female, fertile; limb rather short and wide, white or yellow; tube more or less flattened. Disc corolla 5-lobed, more or less flattened, basally slightly saccate around the cypsela especially adaxially, white, yellow, or pink. Cypselas dorsiventrally flattened, with two lateral ribs with vascular strands, a third adaxial vascular strand rarely present. Pappus absent. Amides present.

DISTRIBUTION. Europe and temperate Asia, some species also in N. Africa, a few species, in general *A. millefolium* (s. l.) naturalized in N. America and also in the S. hemisphere; most species in SE Europe and SW Asia. – 115 spp.

Achillea is a large genus, but with respect to floral characters, homogeneous and well defined. The cypselas are flattened and thin-walled with 2 lateral ribs and the corolla is basally slightly saccate around the cypsela (Khandzhyan, 1983). The list of species is compiled from standard floras.

A. abrotanoides (Vis.) Vis. SE Europe.
A. absinthoides Hal. SE Europe (Greece).
A. acuminata (Ledeb.) Schultz-Bip. E. Siberia, Far East, Mongolia, China, Japan.
A. aegyptiaca L. SE Europe (Greece).
A. ageratifolia (Smith in Sibth. & Smith) Boiss. SE Europe.
A. ageratum L. S. Europe and N. Africa in Morocco.
A. aleppica DC. Turkey, Middle East, Iraq, Iran.
**A. alpina* L. E. Siberia, Far East, Mongolia, China, Himalayas.
**A. ambrosiaca* (Boiss. & Heldr.) Boiss. SE Europe (Greece).
A. arabica Kotschy. Middle East.
**A. asiatica* Serg. C. Asia, Siberia, Far East, Mongolia, China.
A. asplenifolia Vent. E. Europe.
A. atrata L. C. Europe.
A. aucheri Boiss. Iran.
A. barbeyana Heldr. & Heimerl in Heimerl. SE Europe (Greece).
A. barrelieri (Ten.) Schultz-Bip. S. Europe (Italy).
A. biebersteinii Afan. (*A. micrantha* Willd., *A. micranthoides* Klokov). E. Europe, S. European Russia, Turkey, Caucasus, Middle East, Iran, Afghanistan, C. Asia.
A. biserrata M. Bieb. Caucasus.
**A. boissieri* (Hausskn.) Boiss. Turkey.
**A. brachyphylla* Boiss. & Hausskn. in Boiss. Turkey.
**A. bucharica* Winkler. C. Asia.

A. callichroa Boiss. Iran.
A. camtschatica Rupr. ex Heimerl. E. Siberia.
A. cappadocica Hausskn. & Bornm. Turkey.
A. cartilaginea Ledeb. ex Reichenb. (*A. septentrionalis* (Serg.) Botsch.). E. Europe, Siberia, C. Asia.
A. chamaemelifolia Pourret. SW Europe.
A. chrysocoma Friv. SE Europe.
A. clavennae L. C. and SE Europe.
A. clypeolata Sibth. & Smith SE Europe.
A. coarctata Poiret in Lam. SE Europe, Turkey.
A. collina J. Becker ex Reichenb. C. and SE Europe.
A. compacta Willd. SW Europe, S. Russia.
A. conferta DC. Syria, Iraq, Iran.
A. cretica L. SE Europe, Cyprus, Turkey.
A. crithmifolia Waldst. & Kit. C. and SE Europe.
**A. cucullata* (Hausskn.) Bornm. Turkey.
**A. cuneatiloba* Boiss. & Buhse. Caucasus, Iran.
**A. decolorans* Schrader. Turkey.
A. depressa Janka. E. and SE Europe.
A. distans Waldst. & Kit. ex Willd. C. Europe.
A. erba-rotta All. C. and SE Europe.
A. falcata L. Turkey, Middle East, Iraq.
A. filipendulina Lam. Caucasus, Iran, Afghanistan, C. Asia.
A. fraasii Schultz-Bip. Turkey, SE Europe.
A. fragrantissima (Forssk.) Schultz-Bip. N. Africa in Egypt, Middle East, Iraq.
A. gerberi Willd. W. Asia, S. Europe, Russia.
A. glaberrima Klokov. S. European Russia.
A. goniocephala Boiss. & Bal. in Boiss. Turkey.
A. grandifolia Friv. SE Europe, Turkey.
A. griseo-virens Albov. Caucasus.
A. gypsicola Huber-Mor. Turkey.
A. holosericea Sibth. & Smith. SE Europe.
A. impatiens L. E. Europe (Romania), Siberia, China.
A. inundata Kondr. in Wissjul. S. European Russia.
**A. japonica* Heimerl. Far East, China, Japan.
**A. kellalensis* Boiss. & Hausskn. in Boiss. (*A. haussknechtii* Boiss.). Iran.
A. kotschyi Boiss. Turkey.
**A. latiloba* Ledeb. ex Nordm. Caucasus.
**A. ledebourii* Heimerl. S. Siberia, China.
A. leptophylla M. Bieb. E. Europe, S. European Russia, N. Africa in Morocco and Algeria.
A. ligustica All. S. Europe, N. Africa in Morocco, Algeria and Tunisia.
A. lingulata Waldst. & Kit. SE Europe.
A. lucana Pign. Italy.
A. lycaonica Boiss. & Heldr. in Boiss. Turkey.
**A. macrocephala* Rupr. Far East, Japan.
A. macrophylla L. C. Europe.
A. magnifica Huber-Mor. Turkey.
A. maura Humbert. N. Africa in Morocco.
A. membranacea (Labill.) DC. Turkey, Middle East, Iraq.
A. millefolium L. (*A. lanulosa* Nutt., *A. sudetica* Opiz). Widespread in Eurasia and N. America, introduced in Australia and New Zealand.
**A. monocephala* Boiss. & Bal. in Boiss. Turkey.
A. multifida (DC.) Boiss. Turkey.
A. nana L. C. Europe.
A. nobilis L. (*A. neilrichii* A. Kerner). S. and C. Europe, European Russia, W. Siberia, Turkey, Caucasus, Iran, C. Asia.
A. ochroleuca Ehrh. E. Europe.
A. odorata L. C. and SW Europe, N. Africa in Morocco and Algeria.
A. oligocephala DC. Turkey, Middle East, Iraq, Iran.
A. oxyloba (DC.) Schultz-Bip. C. and E. Europe.
A. oxyodonta Boiss. Iran.
**A. pachycephala* Rech. f. Iran.
A. pannonica Scheele. C., E. and SE Europe.
A. phrygia Boiss. & Bal. in Boiss. Turkey.
A. pindicola Hausskn. SE Europe (Greece).
**A. pseudoaleppica* Huber-Mor. Turkey.
A. ptarmica L. Widespread in Eurasia, introduced in N. America.
A. ptarmicifolia (Willd.) Rupr. ex Heimerl. Caucasus.
A. ptarmicoides Maxim. E. Siberia, Far East, China, Japan.
A. pyrenaica Sibth. ex Godron in Gren. & Godron. SW Europe.
A. roseo-alba Ehrend. C. Europe.
**A. sachokiana* Sosn. Caucasus.
A. salicifolia Besser. European Russia, Siberia, C. Asia, China.
A. santolina L. Throughout N. Africa, Middle East, Iraq, Pakistan.
A. santolinoides Lagasca. SW Europe, N. Africa in Morocco and Algeria.
**A. schischkinii* Sosn. Turkey, Caucasus.
**A. sedelmeyeriana* Sosn. Caucasus.
**A. serbica* Nyman (*A. schurii* Schultz-Bip.). SE Europe.
A. setacea Waldst. & Kit. S., C. and SE Europe, European Russia, S. Siberia, Turkey, Iran, Afghanistan, C. Asia, China.
A. sibirica Ledeb. Siberia, Japan, N. America in Alaska and Canada.
A. sieheana Stapf. Turkey.
A. sintenisii Huber-Mor. Turkey.
A. sipikorensis Hausskn. & Bornm. Turkey.
**A. spinulifolia* Fenzl ex Boiss. Turkey.
A. stricta (Koch) Schleicher ex Gremli. C. Europe.
A. talagonica Boiss. (*A. oxylepis* Boiss. & Hausskn. in Boiss.). Iran.
A. tanacetifolia All. Europe.
A. taygetea Boiss. & Heldr. in Boiss. SE Europe (Greece).
A. tenuifolia Lam. Turkey, Caucasus, Iran.
**A. teretifolia* Willd. Turkey.
A. thracica Velen. E. Europe.
A. tomentosa L. SW Europe.
A. umbellata Sibth. & Smith. SE Europe (Greece).
A. vermicularis Trin. Turkey, Caucasus, Iraq, Iran.
**A. virescens* (Fenzl) Heimerl in A. Kerner. SC Europe.
A. wilhelmsii Koch (*A. kermanica* Gand.). Turkey, Caucasus, Syria, Iraq, Iran, Afghanistan, Pakistan, C. Asia.
**A. wilsoniana* Heimerl ex Hand.-Mazz. China.

51. **ANACYCLUS** L., *Sp. pl.*: 892 (1753). Type species: *A. valentinus* L.

Annual or perennial herbs. Leaves alternate, rarely rosulate, pinnatisect. Capitula solitary or laxly corymbose, pedunculate, rarely closely aggregated, radiate or discoid. Receptacle flat to conical, paleate. Ray florets female, fertile; tube flattened, persistent on the cypselas; limb white or yellow, abaxially sometimes reddish. Disc corolla 5-lobed, sometimes slightly zygomorphic with 2 larger lobes; tube somewhat flattened and adaxially slightly saccate. Cypselas dorsiventrally flattened and laterally winged, rather thick-walled,

apically sometimes coroniform, sometimes with myxogenic cells; wings thick and sclerenchymatic. True pappus absent. Amides present.

DISTRIBUTION. Mainly W. Mediterranean; N. Africa, S. Europe and the Middle East. – 12 spp.

Anacyclus was revised and discussed in detail by Humphries (1979), who also indicated *Leucocyclus* as the sister group.

A. clavatus (Desf.) Pers.
A. homogamos (Maire) Humphries
A. inconstans Pomel
A. latealatus Huber-Mor.
A. linearilobus Boiss. & Reuter
A. maroccanus (Ball) Ball
A. monanthos (L.) Thell. (*A. cyrtolepidiodes* Pomel)
A. nigellifolius Boiss.
A. officinarum Hayne
A. pyrethrum (L.) Lagasca
A. radiatus Lois.
A. valentinus L.

52. **LEUCOCYCLUS** Boiss. in *Diagn. pl. orient.* I (II): 14 (1849). Type species: *L. formosus* Boiss.

A perennial herb. Leaves alternate, vermiform, pinnatisect. Capitula solitary, pedunculate, radiate. Receptacle flat to convex, paleate. Ray florets female, fertile; tube flattened, both adaxially and abaxially vaginate around top of cypsela; limb white. Disc corolla 5-lobed; tube flattened, both adaxially and abaxially but not laterally vaginate around top of cypsela. Cypselas dorsiventrally flattened and laterally winged, rather thick-walled; wings thick and sclerenchymatic. Pappus absent.

DISTRIBUTION. SW Asia in Turkey. – Monotypic.

This monotypic genus is the sister group of *Anacyclus*, as shown by Humphries (1979). Recent work by Valent-Vetschera (1982) has indicated that *Leucocyclus* is similar in flavonoid chemistry to certain members of *Achillea* sect. *Santolinoidea*. This is opposed to cypsela morphology, grouping *Leucocyclus* with *Anacyclus*, and requires further investigation.

53. **MECOMISCHUS** Cosson ex Benth. in Benth. & Hook. f., *Gen. pl.* **2**: 418 (1873). Type species: *M. geslini* (Cosson) Cosson (*M. pedunculatus* (Cosson & Durieu) Maire).

Annual or perennial herbs. Leaves alternate or sometimes partly opposite, few-lobed or entire. Capitula solitary, pedunculate, radiate. Receptacle paleate; paleae with a central resin canal. Ray florets neuter; limb white or yellow. Disc corolla 5-lobed, adaxially slightly saccate, with a rather long tube and a partly enervate limb. Cypselas with 1 adaxial and 2 lateral vascular strands, thin-walled, with myxogenic cells. Pappus absent.

DISTRIBUTION. N. Africa in Morocco and Algeria. – 2 spp.

Mecomischus with two rather different species appears to be related to *Chamaemelum*, *Cladanthus*, and *Rhetinolepis*. They all have thin-walled, obovoid, myxogenic cypselas.

M. halimifolius (Munby) Hochr.
M. pedunculatus (Cosson & Durieu) Maire

54. **CHAMAEMELUM** Miller in *Gard. Dict. abr.* 4th edn. (1754). Lectotype: *C. nobile* (L.) All. – *Ormenis* (Cass.) Cass.

Annual or perennial herbs or half-shrubs. Leaves alternate, pinnatifid or variously pinnatisect. Capitula solitary or laxly corymbose, pedunculate, radiate, disciform, or discoid. Receptacle conical or elongated, paleate; paleae flat or often canaliculate, sometimes enclosing florets, often with a central resin canal, glabrous or abaxially pilose. Ray florets female, fertile or sterile; limb white or yellow. Disc corolla 5-lobed, basally saccate around the cypsela especially adaxially, with a rather long tube and a more or less distinct, generally enervate limb. Cypselas obovoid, with 1 adaxial and 2 lateral very thin ribs with vascular strands, thin-walled and covered with myxogenic cells in longitudinal rows. Pappus absent. Amides and particular thiophene derivatives present.

DISTRIBUTION. Mediterranean, from the Canaries in N. Africa and S. Europe to the Middle East. – 6 spp.

The species of *Chamaemelum* were formerly placed in *Ormenis* or as species of *Anthemis* s. l. The generic name *Chamaemelum* of Miller is prior to Cassini's *Ormenis*, however. Cassini distinguished *Ormenis* from *Anthemis* by the basally saccate corolla. Later, it has also been shown that *Ormenis* has a specialized cypsela morphology, different from that of *Anthemis* (Briquet, 1916). *C. fuscatum*, *C. mixtum*, and *C. nobile* (including *Ormenis santolinoides* (Munby) Harling) also differ in embryology; in contrast to *Anthemis* they have the normal monosporic type of embryo sac development (Harling, 1960). When Miller described the genus he included several species now in other genera. Only two of his species are presently classified in *Chamaemelum*, *C. nobile* and *C. mixtum*. The former is more well-known and the latter is the type of *Ormenis*, hence our choice of *C. nobile* as type species of *Chamaemelum*. In *Flora europaea* (Tutin et al., 1976) the three widespread species are recognized under *Chamaemelum* (*C. fuscatum*, *C. mixtum*, *C. nobile*). There are also a number of North African species described from Morocco. Those that seem distinct are transferred from *Ormenis* to *Chamaemelum* following recent treatments of Benedí González (1986, 1988*a*,*b*; see list of species). The North African species are still in need of revision.

C. eriolepis (Cosson ex Maire) Benedí.
**C. flahaulti* (Emb.) Benedí.
C. fuscatum (Brot.) Vasc. (*Anthemis fuscata* Brot., *Anthemis praecox* Link, *Ormenis praecox* (Link) Briq. & Cavill.)
C. mixtum (L.) All. (*Anthemis mixta* L., *Ormenis mixta* (L.) Dumort.)
C. nobile (L.) All. (*Anthemis nobilis* L., *Ormenis nobilis* (L.) Gay)
C. scariosum (Ball) Benedí.

55. **RHETINOLEPIS** Cosson in *Bull. Soc. bot. Fr.* **3**: 707 (1856). Type species: *R. lonadioides* Cosson.

An annual herb, branched from the base; hairs dolabriform. Leaves alternate, entire or few-lobed. Capitula solitary or few closely together, almost sessile, comparatively small, discoid. Receptacle paleate; paleae scarious with a central resin canal, abaxially pilose. Corolla 5-lobed, adaxially shal-

lowly saccate, with a narrow tube and a distinct, enervate limb. Cypselas narrowly obovoid, without ribs, with 1 adaxial and 2 lateral vascular strands, thin-walled, covered with myxogenic cells in longitudinal rows. Pappus absent.

DISTRIBUTION. N. Africa in Algeria, Tunisia, and Libya. – Monotypic.

Rhetinolepis is a curious small annual very different in habit from its relatives *Chamaemelum*, *Cladanthus*, and *Mecomischus*. However, they have a similar specialized cypsela morphology, and many floral characters in common. In North African floras *Rhetinolepis lonadioides* is also often called *Ormenis lonadioides* (Cosson) Maire.

56. **CLADANTHUS** Cass. in *Bull. Sci. Soc. philom. Paris* **1816**: 199 (1816). Type species: *C. arabicus* (L.) Cass.

An annual herb with branches in whorls below the first capitulum. Leaves alternate, below the capitula whorled, pinnatisect. Capitula solitary, sessile, radiate. Receptacle conical, paleate and pilose; paleae canaliculate and half-enclosing cypsela and basal part of corolla, with a central resin canal, pilose on both sides. Ray florets female, sterile; limb yellow, with comparatively large apical lobes. Disc corolla 5-lobed, basally saccate around the cypsela especially adaxially; lobes with acute appendices. Cypselas obovate, laterally flattened with 1 lateral and 2 marginal very thin ribs with vascular strands, thin-walled and covered with myxogenic cells in longitudinal rows. Pappus absent. Amides and particular thiophene derivatives present.

DISTRIBUTION. Mediterranean, S. Spain and N. Africa in Morocco, Algeria, Tunisia, and Libya. – Monotypic.

This species is known as a relative of *Chamaemelum*, which has relatively plesiomorphic characters when compared to *Cladanthus*. The sister group, however, appears to be *Rhetinolepis*, with small discoid capitula. Thus although the two genera seem rather different they both have a similar branching habit and sessile capitula.

8. **ANTHEMIDINAE** Dumort. emend. Bremer & Humphries, **emend. nov.** (Dumortier, *Fl. belg.*: 69 (1827) ('Anthemideae')). Type species: *Anthemis maritima* L.

Herbae annuae vel perennes vel suffrutices. Capitula solitaria vel laxe corymbosa. Receptaculum paleaceum vel interdum epaleaceum. Corolla flosculi disci 5- vel raro 4-lobata tubo plerumque basaliter incrassato. Cypselae plerumque turbinatae parietibus crassis. Pappus coroniformis vel auriculiformis vel nullus. Sacculus embryonis tetrasporus.

Annual or perennial herbs or suffrutices. Leaves pinnatisect to variously lobed, rarely entire. Capitula solitary or laxly corymbose, radiate or rarely disciform or discoid. Receptacle convex to narrowly conical, paleate or sometimes epaleate. Ray floret limb white or yellow. Disc corolla 5- or rarely 4-lobed; tube mostly basally swollen in fruit. Cypselas generally turbinate and thick-walled, rarely with myxogenic cells. Pappus a corona, an auricle, or absent. Embryo sac tetrasporic.

DISTRIBUTION (Table 18). Eurasia, N. and E. Africa, some *Anthemis* species widespread as weeds also in the S. hemisphere. – 2 genera, 213 spp.

Table 18 General distribution of Anthemidinae, Chrysantheminae, and genera. x=indigenous, o=introduced.

	N. Am.	Eur-Asia	SW Asia	S. Eur.	N. Afr.	S. Afr.	Austr. N.Zeal.	S. Am.
Anthemidinae	o	x	x	x	x	o		
Anthemis	o	x	x	x	x	o	o	o
Nananthea				x				
Chrysantheminae		x	x	x	x	o	o	o
Chrysanthemum		x	x	x	x	o	o	o
Heteranthemis				x	x			
Ismelia					x			
Argyranthemum					x			

Traditionally subtribe Anthemidinae represents all Anthemideae with a paleate receptacle. In our classification it is essentially restricted to the large genus *Anthemis*, the immediate relatives of which are unknown. Chrysantheminae (s. s.), also with thick-walled cypselas, is a possible sister group candidate. We have also provisionally included the isolated monotypic *Nananthea* in Anthemidinae. The reasons are given below in the discussion of *Nananthea*.

The cladogram also includes the Chrysantheminae. If the matrices of both subtribes are analysed together, *Nananthea* appears as the sister group to Chrysantheminae rather than to *Anthemis*. *Nananthea* and the Chrysantheminae share the annual habit and absence of pappus. We would consider the tetrasporic embryo sac uniting *Nananthea* and *Anthemis* a stronger character than these two characters together, however. The possible relationship of *Nananthea* to *Anthemis* is further discussed under the former genus.

Clades and characters – Fig. 9, Tables 2, 19.

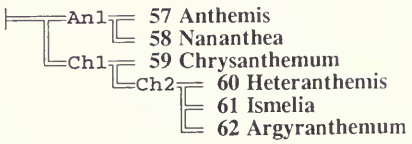

Fig. 9 Cladogram of the Anthemidinae and the Chrysantheminae produced by the *ie* option in Hennig86. Cladogram length = 23, consistency index = 86, retention index = 76.

Table 19 Data matrix for the Anthemidinae and Chrysantheminae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 1 1 1 1 1 1 11 11 1 11 1
	145057655 71480 774271212857 7 15763461321
	532718112 5152812210561022572 6 30065414616
57.*Anthemis*	a1aa111a1 1aa1appp000000000000 ?00ppppp000
58.*Nananthea*	a1aa1?100 1?0001a1000000000000 ????0000p00
59.*Chrysanthemum*	a10a1?1a1 0000010111100000000 ????00000p0
60.*Heteranthemis*	a1001?1a1 1000010111011110000 ????0000000
61.*Ismelia*	11a01?111 0000010111011000110 0 ????0000000
62.*Argyranthemum*	11a01?101 0000000111011000p11 ????00000pp

Clade An1 – subtribe Anthemidinae

175 *Embryo sac tetrasporic.*

Anthemis

11 *Plants with dolabriform hairs.* Many species of *Anthemis* have T- or Y-shaped hairs (Napp-Zinn & Eble, 1980), which occur also in Artemisiinae, Leucantheminae and some genera of Achilleinae.

45 *Receptacle paleate.* Some species of *Anthemis*, subgenus *Ammanthus*, have epaleate receptacles.

82 *Disc corolla tube thickened in fruit.* A thickened corolla tube is characteristic also of many genera in Achilleinae, Leucantheminae and Matricariinae.

108 *Cypselas turbinate.*

Nananthea

1 *Plants annual.*

51 reversed. *Floral parts without resin canals.*

72 *Disc corolla 4-lobed.* This character occurs also within Thaminophyllinae and Matricariinae.

152 reversed. *Cypsela wall not several cell layers thick, not partially or completely sclerified.*

172 *Pappus absent in ray and disc cypselas.*

57. **ANTHEMIS** L., *Sp. pl.*: 893 (1753). Type species: *A. maritima* L.

Annual or perennial herbs or half-shrubs; indumentum frequently of dolabriform hairs. Leaves alternate, pinnatisect to variously lobed, occasionally entire. Capitula solitary or laxly corymbose, pedunculate, radiate or discoid. Receptacle convex to narrowly conical, paleate, rarely basally or totally epaleate; paleae scarious and oblong or subulate, truncate to acute to acuminate, occasionally with a central resin canal. Ray florets female, fertile, or neuter; limb white or rarely yellow or reddish. Disc corolla 5-lobed, yellow or rarely reddish; tube basally much swollen in fruit, rarely pilose; lobes rarely with acute appendices. Cypselas generally turbinate, smooth to prismatic to c. 10-ribbed, sometimes dorsiventrally compressed, sometimes tuberculate, thick-walled, rarely with myxogenic cells. Pappus a shallow, often adaxially more developed corona, or an adaxial auricle, or absent. Embryo sac tetrasporic.

DISTRIBUTION: Europe, Asia, and N. Africa, mainly in S. Europe and SW Asia, one species also in tropical E. Africa (*A. tigrensis*) and 2–3 species widespread as weeds also in N. America and the S. hemisphere (*A. arvensis*, *A. cotula*, *A. tinctoria*). – 211 spp.

The large genus *Anthemis* is, despite its size, morphologically homogeneous and the numerous species stick together in a number of groups. As a whole the genus also appears to be monophyletic based on its turbinate (obconical, in some derived species more obovoid), thick-walled fruits and the invariably basally swollen corolla tube. The south-east European species with an epaleate receptacle, hence earlier classified in a separate genus *Ammanthus*, have now been transferred to *Anthemis* (Greuter, 1968). *Ammanthus* is treated by Fernandes in *Flora europaea* (Tutin et al., 1976) as a subgenus and it represents a monophyletic group of derived species within *Anthemis*. The infrageneric classification of *Anthemis* follows the common pattern with recognition of a number of apomorphic sections and subgenera in addition to a plesiomorphic and probably paraphyletic subgenus *Anthemis*. Yavin (1970, 1972) has proposed an elaborate infrageneric classification of *Anthemis*. She also revised section *Maruta*.

Anthemis was typified with *A. maritima* by Britton & Brown (1913). Later Green (in Hitchcock & Green, 1929) proposed *A. arvensis* as type species, since it is a well-known species also occurring in Sweden, the home-country of Linnaeus. Both species fit Linnaeus' generic description in *Genera plantarum* (Linnaeus, 1757). Linnaeus did not coin the generic name; it was adopted from Micheli (1729) who included *A. maritima* but not *A. arvensis*. Hence, we consider the original typification with *A. maritima* by Britton & Brown to be the correct choice.

A. aaronsohnii Eig. Middle East.
**A. abagensis* Fed. Caucasus.
A. abrotanifolia (Willd.) Guss. Greece.
A. aciphylla Boiss. Turkey.
**A. adonidifolia* Boiss. Turkey.
**A. aeolica* Lojac. Italy.
A. aetnensis Schouw in Sprengel. Italy.
A. alpestris (Hoffsgg & Link) R. Fernandes. SW Europe.
A. altissima L. S. Europe, Krym, Turkey, Caucasus, Iraq, Iran, Afghanistan, C. Asia.
A. amblyolepis Eig. Turkey, Cyprus, Middle East.
A. ammanthus Greuter. Greece.
A. ammophila Boiss. & Heldr. in Boiss. Turkey.
A. anatolica Boiss. Greece, Turkey.
A. anthemiformis (Freyn & Sint.) Grierson. Turkey.
**A. antilibanotica* Eig. Middle East.
A. antitaurica Grierson. Turkey.
A. arenicola Boiss. Turkey.
**A. argyrophylla* (Hal. & Georgiev) Velen. Bulgaria.
A. armeniaca Freyn & Sint. Turkey.
A. arvensis L. Europe, N. Africa, W. Asia, also widespread as a weed in N. America, S. Africa, Australia and New Zealand.
**A. atropatana* Iranshar. Iran.
A. auriculata Boiss. SE Europe, Turkey.
A. austriaca Jacq. C. and E. Europe, Krym, Turkey, Caucasus, Iran.
A. austro-iranica Rech. f., Aellen & Esfand. Iran.
A. bornmuelleri Stoy. & Acht. (*A. galilaea* Eig). Egypt, Middle East.
**A. bourgaei* Boiss. & Reuter. Spain, Morocco.
A. boveana Gay. N. Africa in Morocco, Algeria and Libya.
**A. brachmannii* Boiss. & Heldr. in Boiss. Greece.
A. brachycarpa Eig. Middle East.
A. brachystephana Bornm. & Gauba. Iran.
A. brevicuspis Bornm. (*A. feinbruniae* Eig., *A. rayatensis* Eig). Middle East, Iraq, Iran.
**A. breviradiata* Eig. Middle East.
**A. bulgarica* N. N. Thin. Bulgaria.
**A. bushehrica* Iranshahr. Iran.
A. calcarea Sosn. Turkey, Caucasus.
A. candidissima Willd. ex Sprengel. Caucasus, Iran, C. Asia.
A. carpatica Waldst. & Kit. ex Willd. C. and S. Europe.
A. chia L. SE Europe, Middle East, Egypt.
A. chrysantha Gay. Spain, Algeria.
A. coelopoda Boiss. SE Europe, Turkey, Middle East, Iran, Afghanistan.
A. cornucopiae Boiss. Middle East.

A. corymbulosa Boiss. & Hausskn. in Boiss. Middle East.
A. cotula L. Europe, N. Africa, W. Asia, also widespread as a weed in America, S. Africa, Australia and New Zealand.
**A. cretacea* Zefirov. Krym, Caucasus.
A. cretica L. (*A. anahytae* Woronow ex Sosn., *A. iberica* M. Bieb., *A. montana* L., *A. panachaica* Hal., *A. pindicola* Heldr. ex Hal., *A. ptarmiciformis* K. Koch, *A. tempskyana* Freyn & Sint.). S. Europe, N. Africa, Turkey, Middle East, Iran.
A. cuneata Huber-Mor. & Reese. Turkey.
**A. cypria* Boiss. Cyprus.
A. cyrenaica Cosson. Libya.
A. damascena Boiss. & Gaill. Middle East.
A. davisii Yavin. Turkey.
A. debilifolia Eig. Middle East.
A. deserticola H. Kraschen. & Popov. C. Asia.
A. deserti-syriaci Eig. Middle East.
**A. didymaea* Mout. Middle East.
A. dipsacea Bornm. Turkey.
**A. dubia* Steven. Krym.
A. edumea Eig. Middle East.
A. eliezrae Eig. Middle East, Egypt.
A. emasensis Eig. Middle East.
A. emiliae Sosn. Caucasus.
A. filicaulis (Boiss. & Heldr.) Greuter. Greece.
A. fimbriata Boiss. Turkey.
A. flexicaulis Rech. f. Greece.
A. freitagii Iranshahr. Afghanistan.
A. fruticulosa M. Bieb. Caucasus.
A. fulvida Grierson. Turkey.
A. fumariifolia Boiss. Turkey.
**A. fumarioides* Hochst. Middle East.
**A. fungosa* Boiss. & Hausskn. Iran.
A. gaudium-solis Velen. Bulgaria.
A. gayana Boiss. Iran.
A. gerardiana Jordan. France.
A. gilanica Boiss. Iran.
**A. gilletti* Iranshahr. Iraq, Iran.
A. glaberrima (Rech. f.). Greuter. Greece.
A. glareosa Durieu & Barratte. Libya.
**A. gracilis* Iranshahr. Iran.
A. grossheimii Sosn. Caucasus.
A. halophila Boiss. & Bal. in Boiss. Turkey.
**A. hamrinensis* Iranshahr. Iraq.
A. handel-mazzettii Eig. Middle East.
A. haussknechtii Boiss. & Reuter in Boiss. Syria, Iraq, Iran.
A. hebronica Boiss. & Kotschy. Middle East, Egypt.
A. hemistephana Boiss. Middle East, Iran.
**A. hermonis* Eig. Middle East.
**A. hinkovae* N. N. Thin. Bulgaria.
A. hirtella Winkler. C. Asia.
A. homalolepis Eig. Middle East.
A. hyalina DC. Turkey, Middle East, Iraq, Iran.
A. hydruntina Groves. Italy.
A. indurata Del. Middle East, N. Africa in Egypt and Libya.
A. ismelia Lojac. Italy.
**A. jailensis* Zefirov. Krym.
**A. jordanovii* Stoy. & Acht. Bulgaria.
A. kandaharica Iranshahr. Afghanistan, Pakistan.
**A. karabaghensis* Mikheev. Caucasus.
A. kitanovii N. N. Thin. Bulgaria.
A. kitenensis N. N. Thin. Bulgaria.
A. kotschyana Boiss. Turkey, Middle East, Iraq, Iran.
**A. krugeriana* Pampan. Libya.
**A. kurdica* Iranshahr. Iraq.
**A. kuzmanovii* N. N. Thin. Bulgaria.
A. laconica R. Franzén. Greece.
**A. leptophylla* Eig. Iraq, Iran.
A. leucanthemifolia Boiss. & Blanchet. Middle East, Egypt.
A. leucolepis Eig. Middle East.
**A. linczevskyi* Fed. C. Asia.
**A. lithuanica* (DC.) Besser ex Trautv. Europe in Lithuania and Russia.
A. lorestanica Iranshahr. Iran.
A. lyonnetioides (Boiss. & Kotschy) Boiss. Middle East.
**A. macedonica* Boiss. & Orph. in Boiss. SE Europe.
A. macrantha Heuffel. SE Europe.
**A. macroglossa* Sommier & Levier. Caucasus.
A. maris-mortui Eig. Middle East.
**A. maris-nigri* Fed. Caucasus.
A. maritima L. SW Europe, N. Africa.
**A. markhotensis* Fed. Caucasus.
A. marschalliana Willd. Caucasus.
A. mauritiana Maire & Sennen. Morocco.
A. mazandaranica Iranshahr. Iran.
A. melampodina Del. (*A. deserti* Boiss.) Middle East, Egypt.
A. melanacme Boiss. & Hausskn. in Boiss. Turkey, Middle East.
A. melanoloma Trautv. Turkey.
**A. meteorica* Hausskn. Greece.
A. micrantha Boiss. & Hausskn. Iraq.
A. microcephala (Schrenk) B. Fedtsch. (*A. straussii* Bornm., *A. tenuiflora* Gilli). C. Asia, Iraq, Iran, Afghanistan.
A. microlepis Eig. Middle East.
A. microsperma Boiss. & Kotschy. Middle East, Egypt.
**A. mirheydari* Iranshahr. Iran.
A. moghanica Iranshahr. Iran.
**A. monantha* Willd. Krym.
**A. monilicosta* Pomel. N. Africa in Morocco, Algeria and Libya.
A. muricata (DC.) Guss. Italy.
**A. nabataea* Eig. Middle East.
A. odontostephana Boiss. (*A. tubicina* Boiss. & Hausskn. in Boiss.). Iran, C. Asia.
**A. orbelica* Pancic. Bulgaria.
A. orientalis (L.) Degen (*A. pectinata* (Bory & Chaub.) Boiss. & Reuter). Greece, Turkey.
A. oxylepis (Boiss.) Boiss. Turkey.
A. palestina Reuter in Boiss. (*A. melanolepis* Boiss., *A. syriaca* Bornm.). Turkey, Cyprus, Middle East, SE Europe.
A. parnassica (Boiss. & Heldr.) R. Fernandes. SE Europe.
A. parnesia Boiss. & Heldr. in Boiss. Greece.
**A. parviceps* Dobrocz. & Fed. Krym.
A. parvifolia Eig. Middle East.
**A. patentissima* Eig. Middle East.
A. pauciloba Boiss. Turkey, Iraq.
A. pedunculata Desf. N. Africa in Morocco, Algeria and Libya.
A. persepolitana Boiss. Iraq, Lebanon, Syria.
A. persica Boiss. Iran.
A. pestalozzae Boiss. Turkey.
A. plebeia Boiss. & Noë. Iraq.
**A. plutonia* Meikle. Cyprus.
A. pseudocotula Boiss. (*A. behboudiana* Rech. f. & Esfand.). Turkey, Cyprus, Middle East, Iraq, Iran, N. Africa in Egypt and Libya.

A. punctata Vahl. Italy, N. Africa in Morocco, Algeria and Tunisia.
**A. pungens* Yavin. Turkey.
A. rascheyana Boiss. Middle East.
**A. regis-borisii* Stoy. & Acht. Bulgaria.
A. retusa Del. Egypt.
**A. rhodensis* Boiss. Turkey.
**A. rhodocentra* Iranshahr. Iran, Afghanistan, Pakistan.
A. rigida (Sibth. & Smith) Boiss. & Heldr. SE Europe, Turkey, Cyprus.
A. rosea Smith in Sibth. & Smith. Turkey.
A. rumelica (Velen.) Stoy. & Acht. Bulgaria.
A. ruthenica M. Bieb. C. and SE Europe, Caucasus.
A. sabulifolia Pomel. N. Africa.
A. saguramica Sosn. Caucasus.
A. samuelssonii Rech. f. Middle East.
A. sancti-johannis Turrill. Bulgaria.
**A. saportana* Albov. Caucasus.
A. scaettae Pampan. Libya.
A. scariosa Banks & Sol. in Russell. Turkey, Middle East, Iraq, Iran.
**A. schischkiniana* Fed. Caucasus.
A. schizostephana Boiss. & Hausskn. Iraq, Iran.
A. scopulorum Rech. f. Greece.
A. scrobicularis Yavin. Middle East.
A. secundiramea Biv. SW Europe, N. Africa in Algeria and Tunisia.
A. segetalis Ten. (*A. brachycentros* Gay ex W. Koch). S. Europe.
A. semiensis Pichi-Serm. Ethiopia.
A. sibthorpii Griseb. Greece.
A. sintenisii Freyn. Turkey.
A. sosnovskyana Fed. Caucasus.
A. spruneri Boiss. & Heldr. in Boiss. Greece.
A. sterilis Steven. Krym.
A. stiparum Pomel. N. Africa.
**A. stribrnyi* Velen. Bulgaria.
**A. susiana* Náb. Iraq, Iran.
A. talyschensis Fed. Caucasus, Iran.
**A. taubertii* Durieu & Barratte. Libya.
A. tenuicarpa Eig. Middle East.
A. tenuiloba (DC.) R. Fernandes. SE Europe.
A. tigrensis Gay ex A. Richards. E. Africa.
A. tinctoria L. (*A. debilis* Fed., *A. euxina* Boiss., *A. subtinctoria* Dobrocz.). Europe, W. and C. Asia, also naturalized in N. America.
A. tomentella Greuter. Greece.
A. tomentosa L. (*A. peregrina* L.). SE Europe, Turkey.
**A. tranzcheliana* Fed. Krym.
A. tricolor Boiss. Cyprus.
A. tricornis Eig. Turkey.
A. tripolitana Boiss. & Blanchet in Boiss. Middle East.
A. triumfettii (L.) DC. in Lam. & DC. (*A. dumetorum* Sosn., *A. khorassanica* Rech. f., *A. rigescens* Willd.). S. Europe, Turkey, Caucasus, Iran.
A. trotzkiana Claus ex Bunge. S. Russia, C. Asia.
A. tuberculata Boiss. Spain.
**A. virescens* Velen. Bulgaria.
A. wallii Huber-Mor. & Reese. Turkey.
**A. werneri* Stoy. & Acht. Greece.
A. wettsteiniana Hand.-Mazz. Iraq, Iran.
A. wiedemanniana Fischer & C. Meyer. Caucasus, Turkey.
A. woronowii Sosn. Caucasus.
A. xylopoda O. Schwarz. Turkey.
A. yemenensis Podl. Yemen.
**A. zephyrovii* Dobrocz. Krym.
A. zoharyana Eig. Middle East, Egypt.
A. zyghia Woronow. Caucasus.

58. **NANANTHEA** DC., *Prodr.* **6:** 45 (1838). Type species: *N. perpusilla* (Lois.) DC.

A delicate, somewhat succulent, annual herb. Leaves alternate, pinnatifid, with obovate lobes. Capitula solitary, long-pedunculate, very small (2–5 mm diam.), radiate or disciform. Involucre of 5–10 wide bracts in 1 to 2 rows. Receptacle conical, epaleate. Ray florets female, fertile, with or without a white lamina. Disc corolla 4-lobed, with a short tube and large lobes. Cypselas obovoid, with myxogenic cells; ray cypselas with 2 lateral vascular strands; disc cypselas with 2 lateral, 1 adaxial and 1 pseudolateral vascular strand. Pappus absent. Embryo sac tetrasporic.

DISTRIBUTION. S. Europe, Corsica and Sardinia. – Monotypic.

Nananthea is a genus of uncertain position. Traditionally it has been included in a widely circumscribed and heterogeneous *Cotula* group but it shares no synapomorphies with the *Cotula* group, which is part of subtribe Matricariinae, as understood here. *Nananthea* is here provisionally placed together with *Anthemis*, following a suggestion by Reitbrecht (1974). It could be a highly specialized *Anthemis* derivative, related to part of *Anthemis*, possibly subgenus *Ammanthus*. Both genera have tetrasporic embryo sacs. This also occurs in *Tanacetum*, *Tripleurospermum*, and *Heteranthemis*, but *Nananthea* is hardly reminiscent of these genera.

9. **CHRYSANTHEMINAE** Less. emend. Bremer & Humphries, **emend. nov**. (Lessing in *Linnaea* **6**: 167 (1831) ('Chrysanthemeae')). Type species: *Chrysanthemum coronarium* L.

Herbae annuae vel perennes vel suffrutices vel frutices. Capitula solitaria vel laxe corymbosa. Bracteae involucri latae, plurinerves. Receptaculum epaleaceum. Cypselae parietibus crassis, heteromorphae; cypselae flosculorum radii triquetrae, alatae; eae flosculorum disci plerumque lateraliter compressae et abaxialiter adaxialiterque alatae vel raro teretes ad prismaticae. Pappus nullus.

Annual or perennial herbs, half-shrubs or shrubs. Leaves serrate-dentate-pinnatifid to variously dissected. Capitula solitary or laxly corymbose, pedunculate, radiate. Involucral bracts wide, many-veined. Receptacle convex to conical, epaleate. Ray floret limb white and/or yellow. Disc corolla 5-lobed, yellow or rarely red. Cypselas thick-walled, without myxogenic cells, heteromorphic; ray cypselas triquetrous, winged; disc cypselas generally laterally flattened and abaxially and adaxially winged, or rarely terete to prismatic. Pappus absent.

DISTRIBUTION (Table 18). Eurasia, N. Africa and Macaronesia, *Chrysanthemum coronarium* widespread as a weed also in the S. hemisphere. – 4 genera, 28 spp.

Traditionally subtribe Chrysantheminae comprises all of the Anthemideae species with an epaleate receptacle. As circumscribed here it is a small and homogeneous taxon. The close relationship between *Chrysanthemum* s. s. and the three

other genera of this subtribe has also been recognized by earlier authors and is discussed by Humphries (1976).

Clades and characters – Fig. 9, Tables 2 and 19.

Clade Ch1 – subtribe Chrysantheminae

1 *Plants annual. Argyranthemum* consists of shrublets or half-shrubs, here considered a secondary development within the subtribe. A shrubby habit is commonly evolved in island groups.

41 *Involucral bracts wide, flabelliform.* This character also occurs in several genera of other subtribes.

120 *Cypselas heteromorphic; ray cypselas triquetrous, winged; disc cypselas terete to prismatic to laterally flattened.*

172 *Pappus absent in ray and disc cypselas.*

Chrysanthemum

52 reversed. *Ray floret limb not white, but yellow.*

75 *Disc corolla lobes with central resin sacs.*

Clade Ch2

107 reversed. *Cypselas not terete to weakly angled, but acutely angled.*

116 *Disc cypselas laterally flattened.*

121 *Disc cypselas abaxially and adaxially winged.*

Heteranthemis

10 *Plants covered with viscid hairs.*

52 reversed. *Ray floret limb not white, but yellow.*

122 *Cypsela wings as apical spines.*

175 *Embryo sac tetrasporic.* The embryo sac of *Ismelia* is monosporic (Harling, 1951).

182 *Flavonol 5-glycosides present.* Most of the related genera have not been investigated chemically.

Ismelia

55 *Ray floret limb deeply emarginate.*

77 *Disc corolla red.*

Argyranthemum

1 reversed. See clade Ch1.

2 *Plants shrubby.* See clade Ch1 under character 1.

51 reversed. *Floral parts without resin canals.*

176 *Embryo sac disporic.*

59. **CHRYSANTHEMUM** L., *Sp. pl.*: 887 (1753). Type species: *C. coronarium* L.

Annual herbs. Leaves alternate, deeply serrate-dentate and pinnatifid to pectinate, somewhat amplexicaul. Capitula solitary or laxly corymbose, pedunculate, radiate. Involucral bracts wide, many-veined, with resin canals. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow or white distally, many-veined. Ray cypselas triquetrous, laterally winged, adaxially with a narrow wing or ribbed; pappus absent. Disc corolla 5-lobed; lobes with central resin sacs. Disc cypselas prismatic with a narrow adaxial wing or terete, with a thick undulating wall, thus apparently ribbed; pappus absent.

DISTRIBUTION. Europe, Asia and N. Africa, *C. coronarium* widespread as a weed. – 2 spp.

The adaxial cypsela wings of *C. coronarium* are similar to those in *Heteranthemis*, *Ismelia*, and *Argyranthemum*, whereas *C. segetum* has terete disc cypselas and only laterally winged ray cypselas. The adaxial cypsela wing is conceived as a parallelism, since the two species of *Chrysanthemum* are united for example by their corolla lobe resin sacs.

C. carinatum Schousboe is more closely related to *Heteranthemis* and *Argyranthemum* than to the two *Chrysanthemum* species adopted here, and thus it is transferred to *Ismelia*.

C. coronarium L.
C. segetum L.

60. **HETERANTHEMIS** Schott in *Isis, Oken 1818* (5): 822 (1816). Type species: *H. viscidehirta* Schott.

An annual herb covered with viscid glandular hairs. Leaves alternate, serrate-dentate to pinnatifid. Capitula solitary or laxly corymbose, pedunculate, radiate. Involucral bracts wide, many-veined, with resin canals. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow, many-veined. Ray cypselas triquetrous, laterally and adaxially winged; wings projected to apical spines; pappus absent. Disc corolla 5-lobed. Disc cypselas laterally flattened, winged; adaxial wing projected to an apical spine; pappus absent. Embryo sac tetrasporic.

DISTRIBUTION. SW Europe in Spain and Portugal, N. Africa in Morocco and Algeria. – Monotypic.

This species, also known as *Chrysanthemum viscidehirtum* (Schott) Thell., is distinguished from *Ismelia* and *Argyranthemum* by its pubescence of viscid glandular hairs and the apical spines on the cypsela wings.

61. **ISMELIA** Cass. in *Dict. Sci. Nat.* **41:** 40 (1826). Type species: *I. versicolor* Cass. (*I. carinata* (Schousboe) Schultz-Bip.).

An annual herb. Leaves alternate, pinnatisect. Capitula solitary or laxly corymbose, pedunculate, radiate. Involucral bracts wide, many-veined, with resin canals. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb yellow, basally reddish or white, many-veined, deeply emarginate. Ray cypselas triquetrous, laterally and adaxially winged; pappus absent. Disc corolla 5-lobed, red to purple. Disc cypselas laterally flattened, winged; pappus absent.

DISTRIBUTION. N. Africa in Morocco but frequently escaped from cultivation. – Monotypic.

This handsome species, frequently cultivated as an ornamental, is commonly known as *Chrysanthemum carinatum* Schousboe. It is, however, more closely related to *Heteranthemis* and *Argyranthemum* than to *Chrysanthemum coronarium* and *Chrysanthemum segetum*, the two species here retained in that genus. *Ismelia*, *Heteranthemis*, and *Argyranthemum* form a monophyletic group based on their laterally compressed disc cypselas and their especially strongly developed cypsela wings on the adaxial side. Interestingly, Schultz-Bipontinus (1844*b*) expanded the concept of *Ismelia* to

include various Canary Island endemics of *Argyranthemum* (see Humphries, 1976, for details). *Argyranthemum*, however, forms a monophyletic group, so *Ismelia* is related to *Argyranthemum* as a whole rather than to part of it. Uniting *Ismelia* and then by consequence also *Heteranthemis* with *Argyranthemum* because of their similar fruits is hardly desirable, since it necessitates recombination of all *Argyranthemum* specific names, *Argyranthemum* being the youngest name.

62. **ARGYRANTHEMUM** Webb ex Schultz-Bip. in Webb & Berthelot, *Hist. nat. Iles Canaries* **3** (2,2): 245, 258 (1844*b*). Type species: *A. frutescens* (L.) Schultz-Bip.

Shrublets or half-shrubs. Leaves alternate, variously dissected. Capitula solitary or laxly corymbose, pedunculate, radiate. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white, rarely yellow or pink, many-veined. Ray cypselas triquetrous, generally laterally and adaxially strongly winged, sometimes coalesced into groups; wings sometimes reduced, often apically projected to a pappus-like corona; true pappus absent. Disc corolla 5-lobed, yellow; lobes rarely reddish purple. Disc cypselas generally laterally flattened and adaxially and abaxially winged, sometimes prismatic to terete and wingless, sometimes coalesced with ray cypselas, apically often coroniform; true pappus absent. Embryo sac bisporic.

DISTRIBUTION. Macaronesia in the Canary Islands, Madeira (*A. dissectum*, *A. haematomma*, *A. pinnatifidum*), and the Salvage Islands (*A. thalassophilum*). – 24 spp.

Argyranthemum was revised by Humphries (1976). As already pointed out by him, it is related to *Ismelia* and *Heteranthemis*. *Argyranthemum* has, unlike these genera, evolved into many species with even more specialized sometimes coalesced fruits often with folded wings or sometimes secondarily wingless (Borgen, 1972). A new species, *A. sundingii*, was described by Borgen (1980) and a study of variation within *A. pinnatifidum* was undertaken by Rustan (1981).

A. adauctum (Link) Humphries
A. broussonetii (Pers.) Humphries
A. callichrysum (Svent.) Humphries
A. coronopifolium (Willd.) Humphries
A. dissectum (Lowe) Lowe
A. x escarrei (Svent.) Humphries
A. filifolium (Schultz-Bip.) Humphries
A. foeniculaceum (Willd.) Webb ex Schultz-Bip.
A. frutescens (L.) Schultz-Bip.
A. gracile Schultz-Bip.
A. haematomma (Lowe) Lowe
A. haouarytheum Humphries & Bramwell
A. hierrense Humphries
A. jacobiifolium Kunkel
A. lemsii Humphries
A. lidii Humphries
A. maderense (D. Don) Humphries
A. pinnatifidum (L. f.) Lowe
A. sundingii Borgen
A. sventenii Humphries & Aldridge
A. tenerifae Humphries
A. thalassophilum (Svent.) Humphries
A. webbii Schultz-Bip.
A. winteri (Svent.) Humphries

10. **LEUCANTHEMINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Leucanthemum vulgare* Lam.

Herbae annuae vel perennes vel interdum suffruticosae. Folia saepe serrata-dentata vel interdum pectinata-lobata, trifurcata vel integra. Capitula solitaria, pedunculata. Flosculi disci tubo plerumque incrassato. Cypselae plerumque 10(8–12) vel interdum pauciores costas praebentes, inter costas saepe lacunis vallecularibus et canalibus secretoriis et fasciculis vascularibus (*Leucanthemum* et genera sequentia), in costis plerumque cellulis mucilaginis, instructae. Pappus coroniformis vel adaxialiter auriculiformis vel nullus.

Annual or perennial herbs, sometimes suffruticose; indumentum frequently of dolabriform hairs. Leaves often serrate-dentate, sometimes pectinate-lobed, trifurcate or entire. Capitula solitary, pedunculate, generally radiate or sometimes discoid. Involucral bracts sometimes with dark brown margins, sometimes wide and flabelliform. Receptacle flat to conical, epaleate. Ray floret limb white, yellow or rarely reddish. Disc corolla 5-lobed or rarely 4-lobed; tube generally swollen in fruit. Cypselas mostly 10(8–12)-ribbed, sometimes with fewer ribs, often with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs (*Leucanthemum* group of genera), generally with myxogenic cells along the ribs. Pappus a corona, an adaxial auricle, or absent.

DISTRIBUTION (Table 20): Eurasia and N. Africa, mainly in the Mediterranean region, some *Leucanthemum* species widely introduced, also in N. America and the S. hemisphere. – 16 genera, 75spp.

Leucantheminae consists of one well defined monophyletic subclade, the *Leucanthemum* group of genera, a smaller subclade comprised of *Leucanthemopsis*, *Hymenostemma* and *Prolongoa*, as well as a number of isolated genera of uncertain position, here provisionally included in this subtribe.

The *Leucanthemum* group of genera (71–78; see Fig. 10), are all characterized by their specialized cypsela wall with vallecular lacunae, secretory canals, and vascular strands. Their status as a group has been recognized by several earlier authors (for example, see Briquet, 1916).

Leucanthemopsis is apparently allied to the two Iberian monotypic genera *Hymenostemma* and *Prolongoa*, a relationship that hitherto has not been clearly recognized.

The subtribal description above does not cover all divergent characters of the genera, but applies mainly to the *Leucanthemum* and *Leucanthemopsis* groups.

A relationship between *Leucanthemopsis* and *Leucanthemum* has been suggested several times, e. g. by Heywood (1954, 1976). It is supported by presence of flavonol 5-glycosides in both genera. They are also found in *Coleostephus* and *Plagius* and constitute a possible synapomorphy for the *Leucanthemum* and *Leucanthemopsis* groups. Other genera of these groups have not been investigated chemically, as far as we know.

Included in Leucantheminae are also a number of odd, mainly monotypic genera of uncertain affinity. *Lepidopho-*

Table 20 General distribution of Leucantheminae and genera. x=indigenous, o=introduced.

	N.Am.	Eur-Asia	C.& Asia	E.SW. Asia	S.Eur.	N.Afr.	S.Afr.	Austr. N.Zeal.	S.Am.
Leucantheminae	o	x	x	o	x	x	o	o	o
Lepidophorum					x				
Nipponanthemum			x						
Leucanthemella		x	x						
Nivellea						x			
Phalacrocarpum					x				
Leucanthemopsis		x			x	x			
Hymenostemma					x	x			
Prolongoa					x				
Leucanthemum	o	x		o	x	x	o	o	o
Rhodanthemum					x	x			
Leucoglossum					x	x			
Chlamydophora					x	x			
Chrysanthoglossum						x			
Glossopappus					x	x			
Coleostephus					x	x			
Plagius					x	x			

rum, *Nipponanthemum*, *Leucanthemella*, *Nivellea* and *Phalacrocarpum* are classified in this subtribe mainly because of their serrate-dentate leaves (not in *Nivellea*) but also on account of some floral similarities. These genera have 10(8–12)-ribbed cypselas as in the *Leucanthemum* group. An exception is *Lepidophorum* with 5-ribbed cypselas. The positions of these genera are further discussed under each genus.

There is one most parsimonious cladogram produced from the data matrix. It differs from the cladogram presented by having *Hymenostemma* and *Prolongoa* as the sister group to *Lepidophorum* rather than to *Leucanthemopsis*. However, we have chosen the latter arrangement, which is one step longer. We consider the peculiar pappus (character 165) shared by *Hymenostemma*, *Prolongoa* and *Leucanthemopsis* a stronger character than the annual habit and the loss of brown involucral bracts together (characters 1 and 44), which the former two genera share with *Lepidophorum*.

Clades and characters – Fig. 10, Tables 2, 21.

Clade Le1 – subtribe Leucantheminae

11 *Plants with dolabriform hairs.* Most genera of Leucantheminae, notably those provisionally included in the early part of the account, have dolabriform hairs. The character occurs also in Artemisiinae, *Anthemis* (Anthemidinae), and some genera of Achilleinae. Possibly it is a synapomorphy at a lower level within the tribe.

Lepidophorum

1 *Plants annual.*

45 *Receptacle paleate.*

52 reversed. *Ray floret limb not white, but yellow.*

53 *Ray floret limb golden yellow.* Similar rays occur in subclade Le10 of the *Leucanthemum* group of genera.

133 *Cypselas with costal resin canals or sacs.*

Clade Le2

124 *Cypselas with 10 (8–12) multicellular epicarpic ribs.* Fewer ribs occur in most species of *Leucanthemopsis* and in *Hymenostemma* and *Prolongoa*.

Nipponanthemum

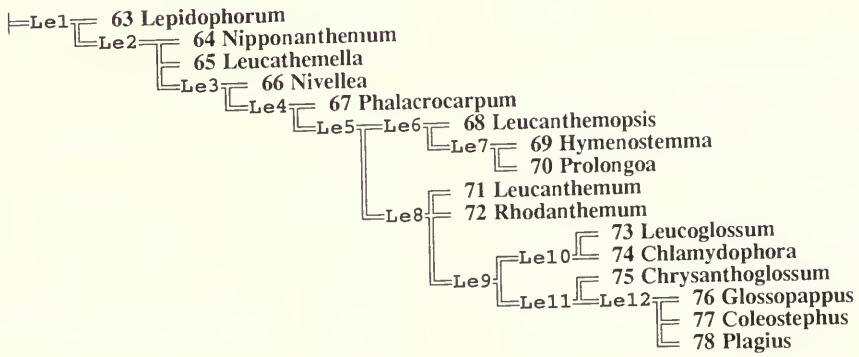

Fig. 10 Cladogram of the Leucantheminae produced by the *bb* option in Hennig86. Cladogram length = 29, consistency index = 58, retention index = 79.

Table 21 Data matrix for the Leucantheminae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1 1 1 1	1 1 1	1 1 1 1 1 1 1 1 1 1 1 1 1	1 1 1 1	1 1 1	1
	1 4 5 0 5 7 6 5 2 1	4 5 3 2	7 8 4 1 0 7 8 6 0 5 7 3 3 6 8 2 2 1 2 3 6 4 7 4 0 2 6	1 5 7 7 7 5 5 5 5 6 6 6 6 6 1 7
	5 3 2 7 1 8 1 1 1	1 1 5 3 3 3 4 2 2 2 4 4 4 4 2 5 3 7 1 4 5 6 4 0 6 0 2 5 8 1 3 1 9 5 9	3 0 5 6 0 5 6 7 9 0 5 6 7 8 5 7
63. *Lepidophorum*	a 1 0 1 1 ? 1 1 1	? 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
64. *Nipponanthemum*	a 1 1 1 1 ? 1 0 1	1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0
65. *Leucanthemella*	a 1 1 1 1 ? 1 1 1	1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0
66. *Nivellea*	1 1 1 1 1 ? 1 1 0	? 1 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? 0 0 ? 0 0 0 0 0 0 0 0 0 0 0
67. *Phalacrocarpum*	a 1 1 1 1 ? 1 1 1	1 0 0 0 0 1 0 1 1 1 1 1 1 1 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0
68. *Leucanthemopsis*	1 1 a 1 1 ? 1 1 0	1 0 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0
69. *Hymenostemma*	1 1 1 1 1 ? 1 1 0	1 1 0 0 0 0 0 0 1 0 0 0 0 ? 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0
70. *Prolongoa*	1 1 0 1 1 ? 1 1 0	1 1 0 0 0 0 0 0 0 0 0 0 0 0 ? 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0
71. *Leucanthemum*	a 1 a 1 1 ? 1 1 1	0 0 0 0 0 1 0 p 1 1 0 0 0 1 0 0 0 0 1 1 a 1 0 0 0 0 p 0 0 0 0 0 0 0	? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
72. *Rhodanthemum*	1 1 1 1 1 ? 1 1 0	? 0 0 0 0 1 0 0 1 1 0 0 0 ? 0 0 0 0 1 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0	? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 p
73. *Leucoglossum*	a 1 1 1 1 ? 1 1 1	? 1 0 0 0 1 0 0 1 0 0 0 0 ? 0 0 0 1 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0	? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0
74. *Chlamydophora*	a 1 ? 1 1 ? 1 1 0	? 1 0 ? 0 1 0 0 1 0 0 0 0 ? 0 0 0 ? 1 1 1 0 0 0 1 1 1 1 0 0 0 0 0 0	? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? 0
75. *Chrysanthoglossum*	1 1 0 1 1 ? 1 1 0	? a 0 1 0 1 0 0 1 0 0 0 0 ? 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 0	? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0
76. *Glossopappus*	a 1 0 1 1 ? 1 1 1	1 1 0 1 0 1 0 0 1 0 0 0 0 ? 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 1 1 0 1 1 1	? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
77. *Coleostephus*	a 1 0 1 1 ? 1 1 1	1 1 0 1 0 1 0 0 1 0 0 0 0 1 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 1 1 0 1 a 0	? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
78. *Plagius*	a 1 ? 1 1 ? 1 1 1	? 0 0 ? 0 1 0 0 1 0 0 0 0 1 0 0 0 ? 1 1 1 0 0 0 0 0 1 0 0 1 0 1 1 0	? ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? 0

2 *Plants shrubby.*

51 reversed. *Floral parts without resin canals.*

Leucanthemella

172 *Pappus absent in ray and disc cypselas.*

Clade Le3

82 *Disc corolla tube thickened in fruit.* This character is sometimes vaguely expressed and absent at least in *Prolongoa.*

Nivellea

1 *Plants annual.*

21 reversed. *Leaves not serrate-dentate.*

172 *Pappus absent in ray and disc cypselas.*

Clade Le4

44 *Involucral bracts with dark brown margins.* This character is absent in several genera (see cladogram) and present in many genera of other subtribes (Cancriniinae, Tanacetinae, Artemisiinae). It may be a synapomorphy at a lower level with reversals in several instances.

Phalacrocarpum

14 *Leaves opposite.*

104 *Disc floret style-branches fused.*

172 *Pappus absent in ray and disc cypselas.*

174 *Testa epidermis cells thick-walled and dark reddish.*

Clade Le5

182 *Flavonol 5-glycosides present.* In this subtribe only *Leucanthemopsis*, *Leucanthemum*, *Coleostephus* and *Plagius* have been investigated for these compounds.

Clade Le6

21 reversed. *Leaves not serrate-dentate.*

124 reversed. See clade Le2.

165 *Pappus a scarious, flimsy corona.*

Leucanthemopsis

There is no autapomorphy for this genus.

Clade Le7

1 *Plants annual.*

44 reversed. See clade Le4.

Hymenostemma

There is no autapomorphy for this genus.

Prolongoa

52 reversed. *Ray floret limb not white, but yellow.*

82 reversed See clade Le3.

103 *Disc floret style-branches long-penicillate.*

157 *Cypsela wall with rod-shaped crystals in small packets.*

171 *Pappus absent in disc cypselas, but present in ray cypselas.*

Clade Le8 – The *Leucanthemum* group of genera

134 *Cypselas with vallecular secretory canals.*

135 *Cypselas with vallecular vascular strands.*

166 *Pappus adaxially long.* In *Chrysanthoglossum* the pappus is coroniform and hardly longer adaxially.

Leucanthemum

11 reversed. *Plants without dolabriform hairs.*

184 *Anthocyanin present in root tips.*

Rhodanthemum

20 *Leaves spathulate in outline, ternate to ternately pinnate.*

21 reversed. *Leaves not serrate-dentate.*

126 *Cypsela ribs protruding, narrow and somewhat wing-like.*

Clade Le9

1 *Plants annual.* The character reverses in *Plagius*, which is perennial.

44 reversed. See clade Le4.

Clade Le10

110 *Cypselas ellipsoid, small,* c.*1 mm long.*

Leucoglossum

171 *Pappus absent in disc cypselas, but present in ray cypselas.*

Chlamydophora

21 reversed. *Leaves not serrate-dentate.*

22 *Leaves entire or apically tridentate.*

35 *Capitula discoid.*

168 *Pappus a large, scarious, adaxial but basally coroniform auricle, as long as the corolla or longer.*

Clade Le11

41 *Involucral bracts wide, flabelliform.* The character reverses in *Plagius*, where the involucral bracts are not flabelliform.

52 reversed. *Ray floret limb not white, but yellow.*

53 *Ray floret limb golden yellow.*

73 *Disc corolla lobes with dorsal appendages.*

Chrysanthoglossum

21 reversed. *Leaves not serrate-dentate.*

141 *Cypselas with dense rows of myxogenic cells also on the corona.*

166 reversed. See clade Le8.

Clade Le12

109 *Cypselas arcuate.*

125 *Cypsela ribs basally fused into a more or less well developed foot callus.* This character is variously strongly expressed in the different species of the three genera involved.

Glossopappus

169 *Pappus a large, scarious, adaxial, flabelliform auricle, as long as the corolla or longer.*

Coleostephus

There is no autapomorphy for this genus.

Plagius

1 reversed. See clade Le9.

35 *Capitula discoid.*

41 reversed. See clade Le11.

63. **LEPIDOPHORUM** Necker ex Cass. in *Dict. Sc. Nat.* **26:** 36 (1823). Type species: *L. repandum* (L.) DC.

An annual or biennial herb. Leaves alternate, oblong to obovate-spathulate, serrate. Capitula solitary, pedunculate, radiate. Involucral bracts wide, many-veined. Receptacle paleate; paleae scarious with a conspicuous resin canal. Ray florets neuter or female, sterile; limb yellow. Disc corolla 5-lobed. Ray cypselas (sterile) flat, with 2 lateral and 1 adaxial resin canal; pappus of *c.* 4 free or basally connate scales. Disc cypselas 5-angled with 5 thin ribs covered with myxogenic cells; pappus absent.

DISTRIBUTION. SW Europe in Spain and Portugal. – Monotypic.

Lepidophorum, formerly a member of *Anthemis* because of its paleate receptacle, is difficult to place. Several authors have suggested a relationship to *Leucanthemum* mainly because of the habitual (foliage) similarities, though *Lepidophorum* does not have the specialized fruits of the *Leucanthemum* group of genera.

Harling (1960) investigated the embryology of many *Anthemis* species, including *A. repanda* (=*Lepidophorum repandum*). *Lepidophorum* has the common (*Polygonum*) type of monosporic embryo sacs, while *Anthemis* proper has tetrasporic embryo sacs. Harling also described the cypselas of *Lepidophorum* in detail and discussed the relationships of the genus. He concluded that *Lepidophorum* should be recognized as a separate genus, not related to *Anthemis* but possibly distantly so to *Coleostephus*, i. e. the *Leucanthemum* group of genera. *Lepidophorum* is here provisionally placed as a basal member of subtribe Leucantheminae, where the *Leucanthemum* group is a subclade (Fig. 10, Le8).

64. **NIPPONANTHEMUM** Kitam. in *Acta phytotax. geobot. Kyoto* **29:** 169 (1978). Type species: *N. nipponicum* (Franchet ex Maxim.) Kitam.

A shrub. Leaves alternate, obovate, apically serrate leaves rather densely set at the ends of the branches. Capitula rather large, solitary, pedunculate, radiate. Involucral bracts wide, many-veined. Receptacle convex, epaleate. Ray florets female, fertile; limb white, many-veined. Disc corolla 5-lobed. Cypselas oblong, 8–10-ribbed, rather thin-walled, without myxogenic cells. Pappus a corona of small scales.

DISTRIBUTION. Japan. – Monotypic.

The monotypic *Nipponanthemum* is based on a handsome species formerly known as *Chrysanthemum nipponicum* Franchet ex Maxim. The position of *Nipponanthemum* is very unclear. It is provisionally placed as an aberrant member of subtribe Leucantheminae. It may on the other hand be more closely related to the relatively plesiomorphic members of Artemisiinae, i. e. *Dendranthema* or certain species in that genus. When he described the genus Kitamura considered it related to *Argyranthemum* but we find no support for his conclusion.

65. **LEUCANTHEMELLA** Tzvelev in Komarov, *Fl. URSS* **26**: 137 (1961). Type species: *L. serotina* (L.) Tzvelev.

Perennial herbs. Leaves alternate, entire or serrate. Capitula solitary or laxly corymbose, pedunculate, radiate. Receptacle convex, epaleate. Ray florets female, sterile; limb white or reddish, many-veined. Disc corolla 5-lobed, with a distinct enervate limb with sessile glands. Cypselas distinctly 7–12-ribbed, without myxogenic cells, with an apical rim but pappus absent.

DISTRIBUTION. E. Europe (*L. serotina*) and Far East, China in Manchuria, Korea and Japan (*L. linearis*). – 2 spp.

This genus is difficult to place (see Dienst, 1983). Tzvelev

also noted its isolated position. In habit it is similar to other members of subtribe Leucantheminae, where it is provisionally placed. It may also be related to *Dendranthema* or some species of that genus. *Leucanthemella* has distinctly many-ribbed, non-myxogenic fruits. This may be related to habitat; the two species grow in marshy places.

L. linearis (Matsum.) Tzvelev
L. serotina (L.) Tzvelev

66. **NIVELLEA** Wilcox, Bremer & Humphries, **gen. nov.** Type species: *N. nivellei* (Braun-Blanquet & Maire) Wilcox, Bremer & Humphries.

Herba annua. Folia lobata sublacerata. Capitula solitaria pedunculata radiata. Receptaculum epaleaceum. Flosculi radiati limbo albo. Flosculi disci tubo basaliter incrassato. Cypselae oblongae, 5–8-costata, sine canalibus secretoriis, sine cellulis mucilaginis. Pappus nullus.

An annual herb. Leaves lobed and rather lacerate. Capitula solitary, pedunculate, radiate. Receptacle flat to convex, epaleate. Ray florets female, fertile; limb white. Disc corolla 5-lobed; tube basally swollen in fruit. Cypselas oblong, 5–8-ribbed, without resin canals and myxogenic cells. Pappus absent.

DISTRIBUTION. N. Africa in Morocco. – Monotypic.

The position of *Nivellea* is difficult to assess. It is superficially similar to some members of the *Leucanthemum* group, e. g. *Leucoglossum*, but does not have the specialized cypselas of that group. It is here provisionally placed as a basal member of subtribe Leucantheminae.

N. nivellei (Braun-Blanquet & Maire) Wilcox, Bremer & Humphries, **comb. nov.** Basionym: *Chrysanthemum nivellei* Braun-Blanquet & Maire in *Bull. Soc. Hist. nat. Afr. N.* **13**: 187 (1922).

67. **PHALACROCARPUM** (DC.) Willk. in *Bot. Ztg* **22**: 252 (1864). Type species: *P. oppositifolium* (Brot.) Willk.

Creeping, suffruticose perennials. Leaves opposite, sheathing, serrate to pinnatifid. Capitula solitary, pedunculate, radiate. Involucral bracts with dark brown margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white or purplish. Central disc florets male (style-branches fused) or neuter. Disc corolla 5-lobed. Cypselas 7–9-ribbed; testa epidermis thick-walled and dark reddish, of elongate-sinuate cells. Pappus absent.

DISTRIBUTION. SW Europe in Spain and Portugal. – 2 spp.

Phalacrocarpum with opposite leaves is in habit and leaf shape similar to other members of Leucantheminae. The subtribal position of this genus must nevertheless be considered provisional.

P. hoffmannseggii (Samp.) Lainz
P. oppositifolium (Brot.) Willk. (*P. anomalum* Cout.)

68. **LEUCANTHEMOPSIS** (Giroux) Heyw. in *An. Inst. bot. A. J. Cavanilles* **32:** 181 (1975). Type species: *L. alpina* (L.) Heyw.

Creeping or caespitose suffruticose perennials. Leaves alternate, serrate to pinnatifid, generally pectinate and spathulate in outline. Capitula solitary, rather long-pedunculate, radiate. Involucral bracts sometimes with dark brown margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white to pinkish or yellow. Disc corolla 5-lobed; tube basally somewhat swollen in fruit. Cypselas 3–10-ribbed, with myxogenic cells especially on the ribs, often with large 2-celled glands. Pappus a scarious flimsy corona. Flavonol 5-glycosides present.

DISTRIBUTION. S. Europe mainly in Spain but extending to SW Russia (*L. alpina*), one species in N. Africa in Morocco (*L. longipectinata*). – 9 spp.

Leucanthemopsis was originally a subsection of *Tanacetum* (sect. *Pyrethrum*), *Tanacetum* then taken in a very wide sense. Heywood (1954, 1976) noted its intermediate position between *Tanacetum* and *Leucanthemum*. Obviously, the *Leucanthemopsis* species could not be accommodated in any of these two large genera, and the subsection was elevated to the rank of genus. New taxa have recently been described by Marchi (1980).

In floral morphology and foliage *Leucanthemopsis* agrees with *Hymenostemma*, a possible sister group. Species of *Leucanthemopsis* are creeping or caespitose suffruticose perennials, whereas *Hymenostemma* is an annual herb. It seems to be the only reliable difference. On the other hand *Hymenostemma* groups with the specialized *Prolongoa*, both being annuals. The three genera clearly form a monophyletic group, but their interrelationships are uncertain. It is also possible that *Leucanthemopsis* is paraphyletic with *Hymenostemma* and *Prolongoa* excluded. The matter requires further study.

L. alpina (L.) Heyw.
L. flaveola (Hoffsgg & Link) Heyw.
L. longipectinata (Font Quer) Heyw.
L. minima (Villars) Marchi
L. pallida (Miller) Heyw.
L. pectinata (L.) Lopéz González & Jarvis (*L. radicans* (Cav.) Heyw.)
L. pulverulenta (Lagasca) Heyw.
L. tatrae (Vierh.) Holub
L. tomentosa (Lois.) Marchi

69. **HYMENOSTEMMA** (Kunze) Willk. in *Bot. Ztg* **22:** 253 (1864). Type species: *H. pseudanthemis* (Kunze) Willk. – *Prolongoa* sect. *Hymenostemma* Kunze, pro parte.

An annual herb. Leaves alternate, pinnatifid-pectinate, spathulate in outline. Capitula solitary, rather long-pedunculate, radiate. Receptacle convex to conical, epaleate. Ray florets female, sterile; limb white. Disc corolla 5-lobed; tube basally swollen in fruit. Cypselas 5–6-ribbed, with myxogenic cells along the ribs. Pappus a scarious, flimsy corona.

DISTRIBUTION. SW Europe in Spain and N. Africa in Morocco. – Monotypic.

Hymenostemma is very similar in habit to *Prolongoa*, though

the latter is distinguished by a number of floral autapomorphies. *Hymenostemma* differs from *Leucanthemopsis* by its annual habit, a feature shared by *Prolongoa*. The sister group relationships of these three genera are somewhat uncertain and it is even possible that *Hymenostemma* and *Prolongoa*, together or separately, have their sister groups within *Leucanthemopsis*.

70. **PROLONGOA** Boiss., *Voyage bot. Espagne* **2**: 320 (1840). Type species: *P. hispanica* Lopéz González & Jarvis.

An annual herb. Leaves alternate, pinnatifid-pectinate, generally spathulate in outline. Capitula solitary, rather long-pedunculate, radiate. Receptacle convex, epaleate. Ray florets neuter; limb yellow; pappus a large flimsy corona. Disc corolla 5-lobed. Style-branches long-penicillate. Cypselas with 1 adaxial and 2 lateral rather thick ribs and 2 abaxial ribs, with myxogenic cells along the ribs; cypsela wall with rod-shaped crystals in small packets; pappus absent.

DISTRIBUTION. SW Europe in Spain. – Monotypic.

Prolongoa has been proposed and now accepted for conservation (Bremer et al., 1987). The species has been known erroneously as *Prolongoa pectinata*, a name that cannot be used since the basionym is a species of *Leucanthemopsis*. *Prolongoa* is related to *Hymenostemma* and *Leucanthemopsis*. The matter is further discussed under these genera. *Prolongoa* has a number of autapomorphies, e. g. a reduced disc floret pappus and more strongly developed cypsela ribs.

71. **LEUCANTHEMUM** Miller, *Gard. Dict. abr.* 4th ed. (1754). Type species: *L. vulgare* Lam.

Perennial herbs with red-tipped roots. Leaves alternate, entire, serrate, or pinnatifid. Capitula solitary or laxly corymbose, pedunculate, radiate or discoid. Receptacle convex or sometimes conical, epaleate. Ray florets female, fertile; limb white, pink, or rarely yellow. Disc corolla 5-lobed; tube basally swollen and spongy in fruit, especially abaxially. Cypselas *c.* 10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells along the ribs. Pappus a corona or an adaxial auricle, sometimes absent. Flavonol 5-glycosides present.

DISTRIBUTION. Throughout Europe but mainly C. and S. parts, one species (*L. discoideum*) also in N. Africa in Morocco, Algeria, and Tunisia, some species (e.g. *L. vulgare*) widespread as weeds. – 33 spp.

With the removal of *L. paludosum* (=*Leucoglossum paludosum*) and *L. arundanum* (=*Rhodanthemum arundanum*) as well as the North African *Leucanthemum* species to *Leucoglossum* and *Rhodanthemum*, *Leucanthemum* becomes morphologically homogeneous and defined by its anthocyanin red root tips. The latter are present in all herbaceous perennials (Favarger, 1966) which now constitute the genus *Leucanthemum* s. s. The genus is a polyploid complex (Villard, 1970).

L. adustum (Koch) Gremli
L. aligulatum Vogt
L. atratum (Jacq.) DC.
L. burnatii Briq. & Cav.
L. catalaunicum Vogt
L. chloroticum A. Kerner & Murb.
L. corsicum (Less.) DC.
L. crassifolium (Lange) Willk. in Willk. & Lange
L. cuneifolium Le Grand ex Coste
L. delarbrei Timb.-Lagr.
L. discoideum (All.) Coste (*L. fontanesii* Boiss. & Reuter, *Chrysanthemum fontanesii* (Boiss. & Reuter) Quezel & Santa)
L. favargeri Vogt
L. gaudinii Dalla Torre
L. gracilicaule (Duf.) Alavi & Heyw.
L. graminifolium (L.) Lam.
L. heterophyllum (Willd.) DC.
L. ircutianum DC.
L. laciniatum Huter, Porta & Rigo
L. lacustre (Brot.) Samp.
L. leucolepis (Briq. & Cav.) Horvatić
L. maestracense Vogt & Hellwig
L. maximum (Ram.) DC.
L. meridionale Le Grand
L. merinoi Vogt & Castroviejo
L. monspeliense (L.) Coste
L. montserratianum Vogt
L. pallens (Gay in Perreymond) DC.
L. praecox (Horvatić) Horvatić
L. pluriflorum Paul.
L. subglaucum De Laramb.
L. sylvaticum (Brot.) Nyman
L. vulgare Lam.
L. waldensteinii (Schultz-Bip.) Pouzar

72. **RHODANTHEMUM** Wilcox, Bremer & Humphries, **comb. et stat. nov**. Type species: *R. arundanum* (Giroux) Wilcox, Bremer & Humphries (*Leucanthemum* sect. *Rhodanthemum* Vogt, *Leucanthemum* subg. *Chrysanthemopsis* Maire, nom. nud.).

Plantae perennes stolonibus saepe tegetes formantes. Folia alterna aggregata rosulata trifida vel ternato-pinnata ut videtur longi-petiolata. Capitula solitaria longepedunculata radiata. Bracteae involucri margine atro-fuscae. Receptaculum convexum epaleaceum. Flosculi radii feminei, vel fertiles vel steriles, limbo albido vel roseo vel rubro vel cremeo-aurantici multi-venoso. Flosculi disci corolla quinquiloba, lutea vel rubra tubo basi inflato et spongioso in fructus maturitate. Cypselae 5–12-costae valleculis lacunis et canaliculis secretoriis cum filis vascularibus et cellulis myxogenis intercostalibus instructis; costae protusae angustae et aliquantum aliformes. Pappus e corona scariosa vel auricula adaxiali basi coroniformi sistens.

Stoloniferous and often mat-forming perennials. Leaves alternate, closely set, becoming rosulate, trifid or ternate-pinnatifid and seemingly long-petiolate. Capitula solitary, with long peduncles, radiate. Involucral bracts with dark brown margins. Receptacle convex, epaleate. Ray florets female, fertile or sterile; limb white, pink, reddish, or creamy orange, many-veined. Disc corolla 5-lobed, yellow or red; tube basally swollen and spongy at maturity of the fruit. Cypselas 5–12-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, and with myxogenic cells along the ribs; ribs protruding,

narrow and somewhat wing-shaped. Pappus with a scarious corona or an adaxial basally coroniform auricle.

DISTRIBUTION. N. Africa in Morocco and Algeria, one species (*R . arundanum*) also in SW Europe in Spain. – 12 spp.

Rhodanthemum (see Vogt, 1991) is a well characterized group of North African, Atlas montane perennials which form mats at relatively high altitudes (700–1200 m). They were formerly classified in *Leucanthemum* or *Chrysanthemum* but are distinguished by a number of synapomorphies.

R. arundanum (Boiss.) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum arundanum* Boiss., *Voy. bot. Espagne* **2**: 317 (1840) (*Leucanthemum arundanum* (Boiss.) Cuatrec., *Leucanthemum mairei* Humbert).

R. atlanticum (Ball) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum atlanticum* Ball in *J. Bot., Lond.* **11**: 366 (1873) (*Leucanthemum atlanticum* (Ball) Maire).

R. briquetii (Maire) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum briquetii* Maire in *Bull. Soc. Hist. nat. Afr. N.* **15**: 88 (1924).

R. catananche (Ball) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum catananche* Ball in *J. Bot. Lond.* **11**: 366 (1873) (*Leucanthemum catananche* (Ball) Maire).

R. depressum (Ball) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum gayanum* var. *depressum* Ball in *J. Linn. Soc.* **16**: 509 (1878) (*Leucanthemum depressum* (Ball) Maire).

R. gayanum (Cosson & Durieu) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum gayanum* Cosson & Durieu in *Bull. Soc. bot. Fr.* **4**: 15 (1857) (*Chrysanthemum gayanum* Ball, *Leucanthemum gayanum* (Cosson & Durieu) Maire).

R. hosmariense (Ball) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum maresii* var. *hosmariense* Ball in *J. Bot. Lond.* **11**: 366 (1873) (*Leucanthemum hosmariense* (Ball) Font Quer).

R. maresii (Cosson) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum maresii* Cosson in *Bull. Soc. bot. Fr.* **4**: 16 (1857) (*Leucanthemum maresii* (Cosson) Maire).

R. maroccanum (Battand.) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: (*Chrysanthemum maroccanum* Battand. in *Bull. Soc. Hist. nat. Afr. N.* **12**: 189 (1921) (*Leucanthemum maroccanum* (Battand.) Maire).

R. mesatlanticum (Emb. & Maire) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum mesatlanticum* Emb. & Maire, *Pl. Maroc Nov. (Arch. Sci. Maroc.*) Fasc. II: 5 (1929).

R. pseudo-catananche (Maire) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum pseudocatananche* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15**:37 (1926).

R. redieri (Maire) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum redieri* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15**:38 (1926).

73. **LEUCOGLOSSUM** Wilcox, Bremer & Humphries, **gen. nov**. Type species: *L. paludosum* (Poiret) Wilcox, Bremer & Humphries – *Prolongoa* sect. *Hymenostemma* Kunze pro parte.

Herbae annuae. Folia dentata-serrata vel pinnatifida. Capitula solitaria radiata. Receptaculum epaleaceum. Flosculi radiati limbo albo vel flavido, basaliter luteo; pappus coroniformis scariosus vel adaxialiter auriculiformis. Flosculi disci corolla parum zygomorpha tubo incrassato; pappus plerumque nullus. Cypselae ellipsoideae parvae 7–10-costatae, inter costas lacunis vallecularibus canalibus secretoriis et fasciculis vascularibus, in costis cellulis mucilaginis instructae.

Annual herbs. Leaves alternate, dentate-serrate to pinnatifid. Capitula solitary, pedunculate, radiate. Receptacle convex or conical, epaleate. Ray florets female, fertile; limb white or pale yellow with a yellowish base; pappus a scarious corona or an adaxial auricle. Disc corolla 5-lobed, slightly zygomorphic; tube basally swollen in fruit. Cypselas ellipsoid, comparatively small, *c.* 1 mm long, 7–10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells along the ribs; generally the pappus is absent.

DISTRIBUTION. SW Europe (*L. paludosum*) in Spain and N. Africa (all species) in Morocco, Algeria, Tunisia, and Libya. – 3 spp.

The type species of this new genus has been recognized as anomalous within *Leucanthemum* e. g. in *Flora europaea* (Tutin et al., 1976). It differs by its annual habit, the small cypselas and the pappus, present in ray florets but absent in disc florets. Together with two North African species it is more closely related to *Chlamydophora*, another annual with small cypselas.

Leucoglossum paludosum is often cultivated as an ornamental.

L. decipiens (Pomel) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum decipiens* Pomel, *Nouv. mat. fl. atl.*: 59 (1860).

L. paludosum (Poiret) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum paludosum* Poiret, *Voy. Barbarie* **2:** 241 (1789). (*Leucanthemum paludosum* (Poiret) Bonnet & Barratte, *Leucanthemum setabense* DC., *Hymenostemma paludosum* (Poiret) Pomel).

L. reboudianum (Pomel) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Leucanthemum reboudianum* Pomel, *Nouv. mat. fl. atl.*: 291 (1860).

74. **CHLAMYDOPHORA** Ehrenb. ex Less., *Syn. gen. Compos.*: 265 (1832). Type species: *C. tridentata* (Del.) Ehrenb. ex Less.

An annual herb. Leaves alternate or basally opposite, entire or tridentate, somewhat fleshy. Capitula solitary, pedunculate, discoid. Receptacle convex, epaleate. Corolla 4- or 5-lobed, yellow or sometimes reddish; tube basally swollen and spongy in fruit. Cypselas ellipsoid, comparatively small, *c.* 1 mm long, 6–10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells on the ribs. Pappus a large, scarious, adaxial but basally coroniform auricle, as long as the corolla or longer.

DISTRIBUTION. N. Africa in Tunisia, Libya, and Egypt, SE Europe in Greece and in Cyprus. – Monotypic.

Chlamydophora is the monotypic and discoid sister group of *Leucoglossum*. The former *C. pubescens* is transferred to *Aaronsohnia*. *C. tridentata* is known also as *Tripleurospermum tridentatum* Hoffm.

75. **CHRYSANTHOGLOSSUM** Wilcox, Bremer & Humphries, **gen. nov**. Type species: *C. trifurcatum* (Desf.) Wilcox, Bremer & Humphries.

Herbae annuae vel raro biennes. Folia pinnatisecta vel saepe trifurcata. Capitula solitaria, pedunculata, radiata. Bracteae involucri latae, plurinerves, flabelliformes. Receptaculum epaleaceum. Flosculi radiati limbo aureo; pappus adaxialiter auriculiformis scariosus vel nullus. Flosculi disci tubo incrassato spongioso in fructu; pappus coroniformis rigidus extus cellulis mucilaginis instructus. Cypselae c. 10-costata, inter costis lacunis vallecularibus canalibus secretoriis et fasciculis vascularibus, in costis et corona cellulis mucilaginis instructae.

Annual or rarely biennial herbs. Leaves alternate, pinnatisect, often trifurcate. Capitula solitary, pedunculate, radiate. Involucral bracts wide, many-veined, flabelliform. Receptacle convex, epaleate. Ray florets female, sterile or sometimes fertile; limb golden yellow, many-veined; pappus a scarious adaxial auricle or absent. Disc corolla 5-lobed; tube basally swollen and spongy in fruit; lobes with appendages; pappus a rather stiff corona with myxogenic cells on the outside. Cypselas dorsiventrally somewhat compressed, c. 10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells along the ribs and also on the pappus.

DISTRIBUTION. N. Africa in Morocco, Algeria, Tunisia and Libya. – 2 spp.

Both species are readily recognizable as sister species by the distinctive leaves and cypselas. *Chrysanthoglossum* is the sister group of the three genera *Glossopappus*, *Coleostephus*, and *Plagius*.

C. deserticola (Murb.) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Pyrethrum deserticola* Murb., in *Acta Univ. lund.* **33**(12): 98 (1897) (*Chrysanthemum deserticola* (Murb.) F. Buxbaum).

C. trifurcatum (Desf.) Wilcox, Bremer & Humphries, **comb. nov**. Basionym: *Chrysanthemum trifurcatum* Desf., *Fl. atlant.* **2**: 281 (1799) (*Leucanthemopsis trifurcata* (Desf.) Alavi).

76. **GLOSSOPAPPUS** Kunze in *Flora*, *Jena* **29:** 748 (1846). Type species: *G. chrysanthemoides* Kunze (*G. macrotus* (Durieu) Briq. in Burnat).

An annual herb. Leaves alternate, serrate-dentate, obovate-spathulate. Capitula solitary, pedunculate, radiate. Involucral bracts wide, flabelliform. Receptacle conical, epaleate. Ray florets female, fertile; limb golden yellow, many-veined. Disc corolla 5-lobed; tube basally much swollen and spongy in fruit, especially abaxially; lobes with appendages. Cypselas somewhat arcuate, 8–10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells along the ribs; basally with a bulbous callus; pappus a large, scarious, adaxial, flabelliform auricle, as long as the corolla or longer.

DISTRIBUTION. SW Europe in Spain and Portugal, N. Africa in Morocco, Algeria and Tunisia. – Monotypic.

Glossopappus macrotus is related to *Coleostephus* and *Plagius*. Possibly *Glossopappus* has its sister group within a paraphyletic *Coleostephus*. The three genera form a monophyletic group. They are further discussed under *Coleostephus*.

77. **COLEOSTEPHUS** Cass. in *Dict. Sci. Nat.* **41:** 43 (1826). Type species: *C. myconis* (L.) Reichenb. f.

Annual herbs. Leaves alternate, serrate-dentate, spathulate. Capitula solitary or laxly corymbose, pedunculate, radiate. Involucral bracts wide, more or less flabelliform. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb golden yellow, many-veined. Disc corolla 5-lobed; tube basally much swollen and spongy in fruit, especially abaxially; lobes with more or less developed appendages. Cypselas arcuate, 8–10-ribbed with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs, with myxogenic cells on the ribs; ribs basally and adaxially fused into a bulbous callus; pappus an oblique, adaxially more or less strongly developed scarious corona. Flavonol 5-glycosides present.

DISTRIBUTION. S. Europe and N. Africa from Morocco to Libya. – 3 spp.

Coleostephus is related to *Plagius* and *Glossopappus* (Alavi, 1968, 1988; Alavi & Heywood, 1976). The six species of these three genera form a monophyletic group but their interrelationships are unclear. *Plagius* with two species is diagnosed by being discoid and perennial (probably secondarily) but these characters are homoplasious and not supported by stronger synapomorphies. The monotypic *Glossopappus* has a specialized large pappus auricle. There is no synapomorphy to diagnose *Coleostephus* from the other two genera and it is possibly paraphyletic. *Coleostephus* and *Plagius* appear to be related by their more arcuate cypselas but the character is variable within *Coleostephus*.

C. multicaulis (Desf.) Durieu (*Chrysanthemum multicaule* Desf.)

C. myconis (L.) Reichenb. f. (*Chrysanthemum myconis* L., *Kremeria myconis* (L.) Maire)

C. paludosus (Durieu) Alavi (*C. clausonis* Pomel, *Chrysanthemum clausonis* (Pomel) Battand., *Kremeria paludosa* Durieu)

78. **PLAGIUS** L'Hérit. ex DC., *Prodr.* **6**: 135 (1838). Type species: *P. ageratifolius* (Desf.) L'Hérit. ex DC. (*P. flosculosus* (L.) Alavi & Heyw.).

Herbaceous or suffruticose perennials. Leaves alternate, serrate-dentate, spathulate. Capitula solitary or laxly corymbose, pedunculate, discoid. Receptacle flat or convex, epaleate. Disc corolla 5-lobed; tube basally swollen and spongy in fruit; lobes with appendages. Cypselas arcuate, c. 10-ribbed, with vallecular lacunae and vallecular secretory canals as well as vascular strands between the ribs; basally with a bulbous callus, with myxogenic cells on the ribs. Pappus an adaxial auricle. Flavonol 5-glycosides present.

DISTRIBUTION. S. Europe in Corsica and Sardinia (*P. flosculosus*) and N. Africa in Algeria and Tunisia (*P. grandis*). – 2 spp.

The two species are very different from each other. Alavi & Heywood (1976) united them into one genus because both are discoid. *P. grandis* is instantly recognizable by the larger solitary capitula on unbranched, basally hairy stems. *P. flosculosus*, by contrast, has smaller capitula on branched stems and it is similar to species of the related genera *Coleostephus* and *Glossopappus*, except for the discoid capitula. *Plagius*, *Coleostephus*, and *Glossopappus* form a monophyletic group but their interrelationships deserve further study (see under *Coleostephus*). The species known as *P. virgatus* (Desf.) DC. is synonymous with *Leucanthemum discoideum*, following Alavi & Heywood (1976).

P. flosculosus (L.) Alavi & Heyw.
P. grandis (L.) Alavi & Heyw. (*Chrysanthemum grandiflorum* (Desf.) Battand.)

11. **THAMINOPHYLLINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Thaminophyllum multiflorum* Harvey

Herbae perennes vel suffrutices vel frutices. Folia serrata vel dentata vel integra vel solum pauciloba. Capitula solitaria, radiata. Cypselae oblongae vel ellipsoideae. Pappus coroniformis vel nullus.

Perennial herbs, half-shrubs or shrubs. Leaves serrate, dentate, entire, or few-lobed only. Capitula solitary, radiate. Receptacle flat to conical, paleate or epaleate, sometimes pilose. Ray floret limb white or yellow. Disc corolla 4- or 5-lobed. Cypselas oblong to ellipsoid, 3–8-ribbed (or angled) or rarely 10-ribbed with costal veins and resin canals (*Adenanthellum*), without or rarely with large myxogenic cells in scattered groups (*Thaminophyllum*). Pappus a corona or absent.

DISTRIBUTION (Table 22). S. Africa. – 5 genera, 17 spp.

Table 22 General distribution of Thaminophyllinae and genera. x=indigenous, o=introduced.

	S. Afr.
Thaminophyllinae	x
Osmitopsis	x
Adenanthellum	x
Inezia	x
Lidbeckia	x
Thaminophyllum	x

This subtribe comprises some small South African genera, which have received little attention in general treatments of the Anthemideae. *Thaminophyllum*, *Lidbeckia*, *Inezia*, and *Adenanthellum* are related as noted by earlier authors. Bond (1980) and Goldblatt (1980) stated that *Thaminophyllum* is related to *Lidbeckia* and *Inezia*. The unusual chromosome number x=10, known in *Thaminophyllum* and *Inezia*, is a feature mentioned by Bond and Goldblatt. *Inezia* was originally described as a *Lidbeckia*. *Adenanthellum* was assumed to be most closely related to *Inezia* by Nordenstam (1976) when he originally described the genus.

Osmitopsis was earlier classified in Inuleae because of the tailed anthers and its proper relationship within Anthemideae has hitherto not been considered. A preliminary chromosome count of 2n=10 as well as remarkable similarities between some species of *Osmitopsis* and the other genera indicate that these genera are related, and it is probable that together they form a monophyletic group. The cladogram is the single most parsimonious one derivable from the data matrix.

Clades and characters – Fig. 11, Tables 2, 23.

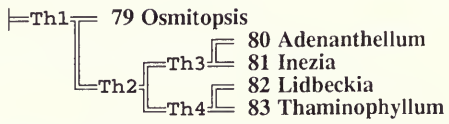

Fig. 11 Cladogram of the Thaminophyllinae produced by the *ie* option in Hennig86. Cladogram length = 25, consistency index = 92, retention index = 80.

Table 23 Data matrix for the Thaminophyllinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 1 1111 11 1 1111
	145057652 745966 5892337574081 24 177675
	532718111 75620157784132928538262 365600
79. *Osmitopsis*	a1111?10a 1111000000000p000p?0p00 ???00p
80. *Adenanthellum*	a1111?111 ?000111111111110000?0000 ??????
81. *Inezia*	a1011?101 100011110000001100?0000 ???00?
82. *Lidbeckia*	11111?100 ?000110000000101111000 ??????
83. *Thaminophyllum*	01111?100 100011000000010111110111 ??????

Clade Th1 – subtribe Thaminophyllinae

51 reversed. *Floral parts without resin canals.* Floral resin canals are present in a number of subtribes and also in Thaminophyllinae, although only in *Adenanthellum*. This is most parsimoniously explained as a reversal for the subtribe with a reappearance in *Adenanthellum*. Clearly, the character is difficult to interpret.

177 *Chromosome number x=10.* The chromosome number is unknown in *Adenanthellum* and *Lidbeckia*, but is nevertheless best interpreted as a synapomorphy for the whole subtribe.

Osmitopsis

45 *Receptacle paleate.*

56 *Ray floret limb epidermis cells tabular (senecioid or mutisioid type).* This ligule epidermis type is uncommon in Anthemideae and reported for example in *Osmitopsis* (Baagøe, 1977).

92 *Anthers caudate.*

Clade Th2

60 *Ray floret tube confluent with the cypsela.*

61 *Ray floret tube persistent on the cypsela.* In *Adenanthellum* and *Inezia* the tube sinus extends to the base and the tube is then virtually absent. Nevertheless the ray corolla, in these cases the limb, is both confluent with and persistent on the cypsela.

Clade Th3

5 *Plants with one or few sparsely branched stems arising from a woody villous caudex.* Some species of *Osmitopsis* are similar to *Adenanthellum* and *Inezia* in this aspect, as mentioned by Nordenstam (1976) when grouping the latter two genera together.

57 *Ray floret tube sinus extending to the base.*

Adenanthellum

51 *Floral parts with resin canals.* See note under clade Th1.

87 *Disc corolla tube confluent with the cypsela.*

98 *Pollen grains hexa-panto-colporate.*

124 *Cypselas with 10 (8–12) multicellular epicarpic ribs.*

131 *Cypselas 10-ribbed with costal veins and resin canals.*

133 *Cypselas with costal resin canals or sacs.* This is characteristic, for example, of *Lepidophorum* in Leucantheminae and large part of Matricariinae but in *Adenanthellum* the cypselas are also 10-ribbed. Whether the resin canals are homologous in the two groups or not is difficult to assess. It is interpreted here as a parallelism.

172 *Pappus absent in ray and disc cypselas.*

Inezia

52 reversed. *Ray floret limb yellow not white.*

59 *Ray floret tube and cypsela pilose laterally; ray floret limb pilose abaxially.* This character also occurs in one of the two *Lidbeckia* species (*L. pectinata*).

72 *Disc corolla 4-lobed.*

Clade Th4

21 reversed. *Leaves not serrate-dentate.*

48 *Receptacle pilose.*

72 *Disc corolla 4-lobed.*

105 *Stylopodium large and persistent in fruit.* This character occurs also in some species of *Osmitopsis*.

172 *Pappus absent in ray and disc cypselas.*

183 *Dehydrofalcarinone and dehydrofalcarinol present.* The other genera of this subtribe are unknown chemically.

Lidbeckia

18 *Leaves with few, oblong to rounded, apically mucronate lobes.*

Thaminophyllum

2 *Plants shrubby.*

15 reversed. *Leaves entire, not variously deeply lobed or divided.*

26 *Leaves closely set, lanceolate to linear.*

142 *Cypselas with large myxogenic cells in rounded, scattered groups.*

79. **OSMITOPSIS** Cass. in *Bull. Sci. Soc. philom. Paris* **1817**: 154 (1817). Type species: *O. asteriscoides* (P. Bergius) Less.

Shrubs or half-shrubs. Leaves alternate, lobed, dentate, serrate, or entire, often glandular-punctate. Capitula solitary or laxly corymbose, radiate. Receptacle flat or convex to conical, paleate. Ray florets female, fertile or sterile, or neuter; tube occasionally pilose; limb white, many-veined, occasionally abaxially pilose; epidermis cells tabular. Disc corolla 5-lobed, glandular. Anthers caudate. Stylopodium sometimes large and persistent in fruit. Cypselas somewhat 3–4-angled or -ribbed. Pappus a corona of subulate to triangular scales, or absent.

DISTRIBUTION. S. Africa in the Cape. – 9 spp.

Until recently *Osmitopsis* has been placed in the Inuleae because of its tailed anthers. The traditional concept of the Anthemideae comprised genera without anther tails, a condition which must be interpreted as a symplesiomorphy, however. Tailed anthers have evolved independently within Anthemideae in the relatively unrelated genera *Osmitopsis*, *Inulanthera* (Gonosperminae), and *Hippolytia* (Tanacetiinae). Stix (1960) showed that *Osmitopsis* has anthemoid pollen and the tribal position in the Anthemideae was confirmed by Bremer (1972) and Reitbrecht (1974).

The position of *Osmitopsis* within Anthemideae has hitherto remained unclear (Heywood & Humphries, 1977). It is placed here in Thaminophyllinae with other small South African genera with similar habit, foliage, many-veined rays, and the less usual chromosome number of x=10. A preliminary count of 2n=20 was made by Bremer (unpubl., on *O. pinnatifida*) but it needs confirmation. Various but not all species of *Osmitopsis* are similar to other genera of subtribe Thaminophyllinae in a number of characters, particularly in habit, pilose and sterile rays, the loss of pappus and a large stylopodium. The genus was revised by Bremer (1972, 1976).

O. afra (L.) Bremer
O. asteriscoides (P. Bergius) Less.
O. dentata (Thunb.) Bremer
O. glabra Bremer
O. nana Schltr
O. osmitoides (Less.) Bremer
O. parvifolia (DC.) Hofmeyr
O. pinnatifida (DC.) Bremer
O. tenuis Bremer

80. **ADENANTHELLUM** B. Nord. in *Bot. Notiser* **132:** 160 (1979). Type species: *A. osmitoides* (Harvey) B. Nord. – *Adenanthemum* B. Nord.

A perennial herb with erect stems from a subterranean caudex. Leaves alternate, serrate, glandular-punctate. Capitula solitary, radiate. Receptacle convex, epaleate. Ray florets female, fertile; limb white, many-veined, confluent with the cypsela; tube absent (sinus extended to the base). Disc corolla 5-lobed, confluent with the cypsela. Pollen hexa-panto-colporate. Cypselas oblong, 10-ribbed, with 10 veins and 10 resin canals. Pappus absent.

DISTRIBUTION. S. Africa in Natal and Transvaal and in Swaziland. – Monotypic.

This recently described monotypic genus has a number of

autapomorphies, notably the unique pollen and the 10-ribbed cypselas with 10 resin canals. In habit and life-form, with a subterranean caudex generating herbaceous flowering stems, it is similar to *Inezia*, as indicated also by Nordenstam (1976) in his original description.

A chromosome number of 2n=30 was reported by Goldblatt (1980) who cited a preliminary, unpublished count by Nordenstam. From that one count (Nordenstam, pers. comm.) it is impossible to tell whether it represents an occasional triploid cell or a triploid specimen or taxon.

The name *Adenanthellum* (Nordenstam, 1979) replaces *Adenanthemum* (Nordenstam, 1976), which turned out to be illegitimate.

81. **INEZIA** E. Phillips in *Bull. misc. Inf. R. bot. Gdns, Kew*: 297 (1932). Type species: *I. integrifolia* (Klatt) E. Phillips.

Perennial herbs with erect stems from a subterranean caudex. Leaves alternate, entire, glandular-punctate. Capitula solitary, radiate. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow, many-veined, abaxially and basally laterally pilose, confluent with the laterally pilose cypsela; tube absent. Disc corolla 4-lobed, glandular. Cypselas oblong, 4-angled. Pappus of minute scales.

DISTRIBUTION. S. Africa in Transvaal and in Swaziland. – 2 spp.

Inezia is based on the transfer of *I. integrifolia* from the related genus *Lidbeckia*. Brusse (1989*a*) has shown that the two genera differ by several floral characters. *Inezia* has a stylopodium of thick-walled cells as compared with thin-walled cells in *Lidbeckia* and the nectaries are conspicuously larger in *Lidbeckia*. Also, there are 9–10 rows of cells in the filament collars of *Lidbeckia* as compared with 5–8 rows of cells in *Inezia*. Both genera have a 4-lobed corolla but nevertheless the sister group of *Inezia* is taken here to be *Adenanthellum* (with a 5-lobed corolla). These two genera have subterranean caudices from which herbaceous stems emerge (Nordenstam, 1976). They also have rays without a tube. It is more parsimonious to place *Adenanthellum* rather than *Lidbeckia* (as well as *Thaminophyllum*) as the sister group of this genus.

I. integrifolia (Klatt) E. Phillips
I. speciosa Brusse

82. **LIDBECKIA** P. Bergius, *Descr. pl. Cap.*: 307 (1767). Type species: *L. pectinata* P. Bergius

Half-shrubs. Leaves alternate, glandular-punctate with few, oblong to rounded, apically mucronate lobes. Capitula solitary, rather long-pedunculate, radiate. Receptacle convex, epaleate, pilose. Ray florets female, sterile, or neuter; limb white, many-veined; sometimes dorsally pilose; tube sometimes laterally pilose, confluent with the sometimes laterally pilose cypsela. Disc corolla 4-lobed, glandular, sometimes pilose; lobes sometimes with short acute appendages. Stylopodium large and persistent in fruit. Cypselas ellipsoid, 3–8-ribbed. Pappus absent. Dehydrofalcarinone and dehydrofalcarinol present.

DISTRIBUTION. S. Africa in the Cape. – 2 spp.

The two species of *Lidbeckia* are related to *Inezia* and *Thaminophyllum*. They are held together as a pair by their similar foliage and habit. *L. quinqueloba* is more pubescent with pilose rays as in *Inezia*. On the other hand both species share a number of synapomorphies, for example the pilose receptacle, with *Thaminophyllum*.

L. pectinata P. Bergius
L. quinqueloba (L. f.) Cass. (*L. lobata* Thunb.)

83. **THAMINOPHYLLUM** Harvey, *Fl. cap.* **3**: 155 (1865). Type species: *T. multiflorum* Harvey

Shrublets. Leaves alternate, closely set, entire, lanceolate to linear, ericoid, glandular. Capitula solitary or laxly corymbose, radiate. Receptacle convex or conical, epaleate, pilose. Ray florets female, sterile; limb white to somewhat purple-pink, many-veined; tube confluent with the cypsela. Disc corolla 4-lobed, glandular; lobes with acute or rounded appendages. Stylopodium large and persistent in fruit. Cypselas ellipsoid, 3–4-angled, with large myxogenic cells in rounded, scattered groups. Pappus absent. Dehydrofalcarinone and dehydrofalcarinol present.

DISTRIBUTION. S. Africa in the Cape. – 3 spp.

Thaminophyllum is a small and distinct genus of ericoid South African shrublets. The sister group is *Lidbeckia*. The two genera differ much in foliage but have a similar floral morphology and they both have a pilose receptacle. The myxogenic cells on the cypselas are of a type different from the common Anthemideae pattern (of rows of large myxogenic cells). In *Thaminophyllum* the myxogenic cells are arranged in rounded groups, scattered on and hardly elevated above the epicarp. *Thaminophyllum* was revised by Bond (1980).

T. latifolium Bond
T. multiflorum Harvey
T. mundtii Harvey

12. **MATRICARIINAE** Bremer & Humphries, **subtrib. nov.**

Type species: *Matricaria recutita* L.

Herbae annuae vel perennes vel suffrutices vel frutices. Capitula saepe solitaria vel raro corymbosa. Receptaculum epaleaceum vel raro paleaceum. Cypselae plerumque 5(4–6)-costatae costis varie dispositis vel interdum dorsiventraliter compressae et lateraliter alatae, plerumque abaxialiter et in costis sed non adaxialiter cellulis mucilaginis instructae. Pappus plerumque adaxialiter longior, coroniformis vel auriculiformis vel e squamis discretis compositus vel nullus.

Annual or perennial herbs, shrublets or shrubs. Leaves often much dissected, sometimes few-lobed or entire or ericoid. Capitula solitary or rarely corymbose, pedunculate or rarely sessile, radiate, disciform or discoid. Receptacle variously shaped, epaleate or rarely paleate. Ray floret limb white or yellow. Outer female florets (in disciform capitula) in one or more rows, sometimes stalked. Disc or central florets 5- or 4-, rarely 3-lobed. Cypselas generally 5(4–6)-ribbed with different rib arrangements or sometimes dorsiventrally flattened and laterally winged, generally with myxogenic cells abaxially and on the ribs but not adaxially. Pappus generally adaxially long, a corona, an auricle, of separate scales, or absent.

DISTRIBUTION (Table 24). Worldwide, most genera in the Mediterranean region and in S. Africa, some *Matricaria*, *Tripleurospermum*, *Cotula* and *Soliva* species widespread as weeds. – 25 genera, 252 spp.

Table 24 General distribution of Matricariinae and genera. x=indigenous, o=introduced.

	N.Am.	Eur-Asia	C.& E. Asia	SW Asia	S.Eur.	N.Afr.	S.Afr.	Austr. N.Zeal.	S.Am.
Matricariinae	x	x	x	x	x	x	x	x	x
Cymbopappus							x		
Pentzia						x	x		
Marasmodes							x		
Rennera							x		
Oncosiphon	o						x		
Otospermum					x	x			
Heteromera						x			
Daveaua					x	x			
Matricaria	x	x	x	x	x	x	o	o	o
Microcephala		x	x						
Endopappus						x			
Myxopappus							x		
Foveolina							x		
Lonas					x	x			
Tripleurospermum	o	x	x	x	x	x	o	o	o
Aaronsohnia		x				x			
Leucoptera							x		
Adenoglossa							x		
Hilliardia							x		
Cotula	x	o			o	x	x	x	x
Leptinella								x	x
Soliva	x	o			o	o		x	x
Schistostephium							x		
Hippia							x		
Eriocephalus							x		

The Matricariinae is our largest subtribe with respect to the number of genera (although the Artemisiinae, with *Artemisia*, contains more species). It consists mainly of a large group of predominantly annual and Mediterranean genera such as *Matricaria* and *Tripleurospermum*, and the predominantly South African *Cotula* group. Various South African genera are related to the Eurasian/North African taxa, for example, the annual genera *Adenoglossa*, *Myxopappus*, *Foveolina*, and possibly *Rennera* and *Oncosiphon*, as well as the South African shrubby genera *Leucoptera*, *Cymbopappus*, *Pentzia* and *Marasmodes*.

The *Cotula* group is more narrowly and distinctly circumscribed here than traditionally. It comprises the last seven genera in this account, characterized by their dorsiventrally flattened fruits. *Hilliardia* and *Eriocephalus* are both isolated and must be regarded as provisionally placed here, however.

The whole subtribe is characterized by the arrangement of myxogenic cells on the cypselas, abaxially and on the ribs, but not on the adaxial surface. Furthermore, they have a pappus that is adaxially long, whether coroniform, auriculiform or of separate scales. Some genera do not have cypselas with myxogenic cells or with a pappus, for example, parts of the *Cotula* group. In the cladogram (Fig. 12) these two characters unite all Matricariinae, except the *Cotula* group, for reasons of parsimony. However, it is possible that they are synapomorphies for the whole subtribe, since they occur also within the *Cotula* group.

The positions of *Oncosiphon* and *Rennera*, both with epappose and non-myxogenic cypselas, are more doubtful. In the absence of synapomorphies with genera of other subtribes they are provisionally retained in Matricariinae. The species of those two genera were formerly classified in *Pentzia* and *Tripleurospermum*. *Rennera* and *Oncosiphon* appear as sister groups in the cladogram. This is because they are similar in their mutual absence of some features, viz. myxogenic cells and pappus. In future studies they may turn out not to be closely related. The matter is further discussed by Källersjö (1988).

The generic interrelationships within the subtribe as shown in the cladogram (Fig. 12) must be regarded as very preliminary. Many of the groupings are supported only by one or a few homoplasious characters, and numerous (226) equally parsimonious solutions are possible. We consider some subclades well supported, however. These include Ma3 with *Cymbopappus*, *Pentzia* and *Marasmodes*, Ma8 *Heteromera* and *Daveaua*, Ma9 *Matricaria* and *Microcephala*, Ma12 *Myxopappus* and *Foveolina*, Ma16 *Leucoptera* and *Adenoglossa*, Ma17 the *Cotula* group of genera (with the possible exclusion of *Hilliardia* and *Eriocephalus*), Ma19 with *Cotula*, *Leptinella*, and *Soliva*, and Ma21 with *Schistostephium*, *Hippia*, and *Eriocephalus* (the last genus possibly to be excluded). All those clades are retained in the strict consensus tree of all the equally parsimonious cladograms found.

Clades and characters – Fig. 12, Tables 2 and 25.

Clade Ma1 – subtribe Matricariinae

In this cladogram there are no synapomorphies for the subtribe but as explained above, characters 140 and 166 of clade Ma2 may be synapomorphies for the subtribe, with reversals in the *Cotula* group (Ma17). They appear as such in the alternative equally parsimonious cladograms.

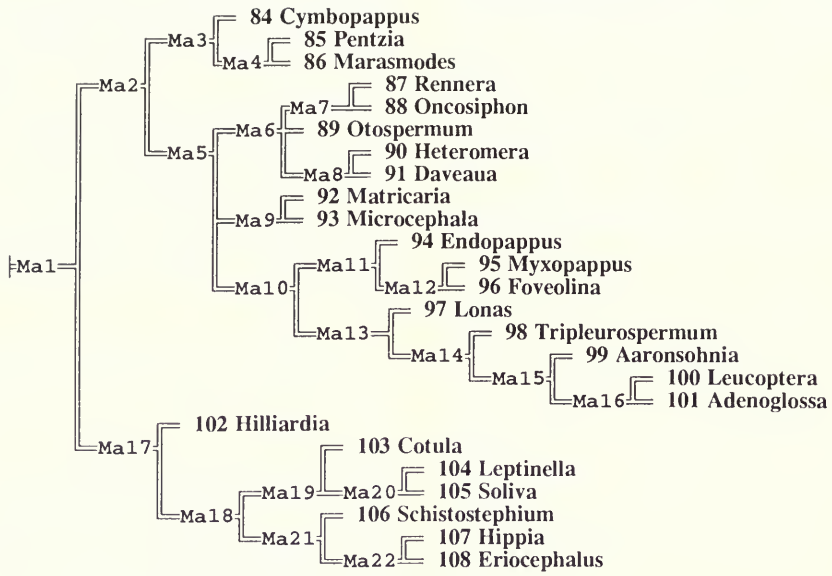

Fig. 12 Cladogram (of 226 possible) of the Matricariinae produced by the *bb* option in Hennig86. Cladogram length = 97, consistency index = 60, retention index = 68.

Table 25 Data matrix for the Matricariinae. 1 = presence, 0 = absence, ? = missing data or not applicable, p = polymorphic but scored as the plesiomorphic condition, a = polymorphic but scored as the apomorphic condition.

	1111 11 1 11 11111111 111 11111 111 1 1 1 1 111 1 1 11
	14505765 46 89333 77578226712174424372433784415541291279760736601545 1755555666671 82
	53271811 06220543132323387359816779059576531126824457564724063711500 3635679056806922
84. *Cymbopappus*	11111?10 11a1100000000000000000000000000?000000000000000000000000? ??00000000000000
85. *Pentzia*	11?11?1p 111111p00pp0000000?00?000000p000?000000000000000000000?0000? ???????????0ppp0
86. *Marasmodes*	a1?11?10 1111111000000000000?00?000000000?000000000000000000000?0000? ????????????00000
87. *Rennera*	11?11?11 0?000100111100000?00?000000000?000000000000000000000?0000? ????????????0000
88. *Oncosiphon*	11111?11 0?010p00111011110000000p00000p000000000000000000000000000? ?0000000000?0000
89. *Otospermum*	11111?11 1100000011000001110000000000000?000000000000000000000000? ??00000000000000
90. *Heteromera*	11111?11 1100000111000000001100000000000?000000000000000000000000? ??00000000000000
91. *Daveaua*	11111?11 1101000111000000001011000000000?000000000000000000000000? ??00000000000000
92. *Matricaria*	11111111 1100000a10p0p00000000p11100p000000000000000000000000p000000? ?00000000000p000
93. *Microcephala*	11111?11 1000p00100000000010000a111000000?000000000000000000000000? ??00000000000000
94. *Endopappus*	11a11?11 1100000010000000000100000010000?0111000000000000000p000000? ??00000000000000
95. *Myxopappus*	10?11?11 110001001000p00000?10?000010000?0100111000000000000?00000 ?0?????????00000
96. *Foveolina*	11111?11 11000p001000p000000a000000100000?000011000000000000p000000? ?00000000000p000
97. *Lonas*	11?11?11 1100010110000000007?10?000010111000000000000000000000000000? ??00000000000000
98. *Tripleurospermum*	11111111 a1000p01a0p0000000010000000ap00111000000000000000000?0000? ???????????00000
99. *Aaronsohnia*	11111?11 11010p0110p0000000000000001100007000000000000000000p000000? ??00000000000000
100. *Leucoptera*	11111?11 1110000100000000000000001a0000?00100001111000000000000000? ??00000000000000
101. *Adenoglossa*	01011?11 1100000110000000000000000100000?00100001111111000000000000? ??00000000000000
102. *Hilliardia*	11111?10 0?10000000101000000000000010000??000000000a0001ap0app0000? ?0000000000?00p0
103. *Cotula*	11111?11 p?000p0ap0101000000000000001p000001000000100a0001011app0000? ????????000?0000
104. *Leptinella*	11111?11 p?000p0a00101000007007?00001p0000??000000a001000?0101111000? ????????000?000p
105. *Soliva*	11?11?1a 0?000010101010000?00?0000100000??000000100000010000000110? ??0000000007?0000
106. *Schistostephium*	a1?11?10 0?100p0000101000007007?000010a000??000000100000000a00a000000? ????????000?0000
107. *Hippia*	11?11?10 0?10000000100000000?00?000010a000??000000100100000101000000? ????????000?0000
108. *Eriocephalus*	11111?10 0?10000000100000000000000010a100?100000010000000010p000001a ??0000000007?0000

Clade Ma2

140 *Cypselas with myxogenic cells on abaxial surface and on the ribs of the adaxial surface.* This character is assumed to be secondarily lost in *Rennera* and *Oncosiphon*. Several species of *Tripleurospermum* are also devoid of myxogenic cells, presumably secondarily. The character occurs also within *Cotula* and *Leptinella*.

166 *Pappus adaxially long.* This character comprises a variety of different but homologous pappus types. The pappus is secondarily lost in *Rennera* and *Oncosiphon*. Some species of *Matricaria*, *Tripleurospermum* and *Pentzia* also lack pappus, presumably secondarily.

Clade Ma3

2 *Plants shrubby.*

51 reversed. *Floral parts without resin canals.*

82 *Disc corolla tube thickened in fruit.* This character is widespread in Achilleinae and Leucantheminae and occurs also in other genera of Matricariinae, notably *Oncosiphon* and *Aaronsohnia*.

90 *Disc corolla tube and and cypsela ribs with thick vascular strands.*

Cymbopappus

There is no clear autapomorphy for this genus.

Clade Ma4

35 *Capitula discoid.*

Pentzia

There is no autapomorphy for this genus.

Marasmodes

34 *Capitula sessile along the stems.*

Clade Ma5

1 *Plants annual.*

Clade Ma6

73 *Disc corolla lobes with dorsal appendages.*

Clade Ma7

140 reversed. See clade Ma2.

172 *Pappus absent in ray and disc cypselas.*

Rennera

35 *Capitula discoid.*

153 *Cypsela thick-walled and conspicuously rugose.*

Oncosiphon

72 *Disc corolla 4-lobed. Cotula* and related genera also have 4-lobed corollas.

82 *Disc corolla tube thickened in fruit.*

83 *Disc corolla tube very thick and brittle.*

123 *Cypselas with a mainly abaxial entire or toothed rim.*

Otospermum

128 *Cypselas with 1 abaxial and 2 lateral thick ribs and 2–3 adaxial ribs.* The arrangement of the three major ribs is abaxial-lateral and thus opposite to that of *Tripleurospermum* and many other genera.

167 *Pappus a stiff adaxial auricle.*

173 *Testa epidermis cells spirally arranged around the embryo.* A similar testa occurs in *Microcephala*.

Clade Ma8

115 *Ray cypselas dorsiventrally flattened with 3 adaxial ribs.*

133 *Cypselas with costal resin canals or sacs.*

Heteromera

129 *Cypselas with 1 adaxial and 2 lateral rather thick ribs.* The same rib arrangement occurs in *Tripleurospermum* and related genera of clade Ma10.

Daveaua

82 *Disc corolla tube thickened in fruit.*

118 *Ray cypselas laterally winged; wings projected to apical teeth.*

171 *Pappus absent in disc cypselas, but present in ray cypselas.*

Clade Ma9

46 *Receptacle narrowly conical to subulate.*

47 *Receptacle hollow.*

127 *Cypselas with 5 mainly adaxially arranged ribs.*

Matricaria

133 *Cypselas with costal resin canals or sacs.*

Microcephala

149 *Cypselas with rather stiff unbranched hairs of 3–8 cells with spiral wall thickenings.*

173 *Testa epidermis cells spirally arranged around the embryo.* A similar testa occurs in *Otospermum*.

Clade Ma10

129 *Cypselas with 1 adaxial and 2 lateral rather thick ribs.* The same rib arrangement occurs also in *Heteromera*. *Foveolina* has rather weak, but similarly arranged ribs.

130 *Cypselas with 2 lateral vascular strands, sometimes also with 1 adaxial strand. Tripleurospermum* has a different autapomorphic type with 5 strands, with 2 abaxial strands associated with the two apical-abaxial resin sacs.

Clade Ma11

141 *Cypselas with dense rows of myxogenic cells also on the corona.* This character is not expressed in *Foveolina*.

Endopappus

41 *Involucral bracts wide, flabelliform.*

107 reversed. *Cypselas not terete to weakly angled or flattened, but sharply angled.*

112 *Cypselas large, with 3 thick protruding sclerenchymatous ribs, somewhat winged in ray cypselas.*

Clade Ma12

156 *Cypsela wall white and spongy; pericarpic cells isodiametric with thin spiral wall thickenings.* (Källersjö, 1988).

158 *Cypsela wall with numerous druses in the pericarp.* (Källersjö, 1988).

Myxopappus

35 *Capitula discoid.*

42 *Involucral bracts subulate.*

43 reversed. *Involucral bracts without scarious margins.*

Foveolina

141 reversed. See clade Ma11.

Clade Ma13

133 *Cypselas with costal resin canals or sacs.*

Lonas

29 *Capitula densely corymbose.*

35 *Capitula discoid.*

45 *Receptacle paleate.*

137 *Cypselas with a single resin sac apically in the adaxial rib.*

Clade Ma14

75 *Disc corolla lobes with central resin sacs.* The character is expressed in most but not all species of *Tripleurospermum*, in *Aaronsohnia* and in *Leucoptera*. It reverses in *Adenoglossa*.

Tripleurospermum

130 reversed. See clade Ma10.

136 *Cypselas abaxially and apically with 2 distinct, occasionally 1 or 3–5, resin sacs.*

175 *Embryo sac tetrasporic.*

183 *Dehydrofalcarinone and dehydrofalcarinol present.* These products in polyacetylene synthesis are common in the Asteraceae but uncommon in Anthemideae, occurring also in *Cotula* and *Eriocephalus*. They may represent a secondarily simplified metabolism (Greger, 1977). The position of the character on the cladogram is uncertain because most genera of the subtribe have not been investigated chemically.

Clade Ma15

129 reversed. See clade Ma10.

Aaronsohnia

82 *Disc corolla tube thickened in fruit.*

Clade Ma16

24 *Leaves rather fleshy, few-lobed or entire.*

41 *Involucral bracts wide, flabelliform.*

95 *Anthers with endothecial tissue partly or wholly polarized.*

114 *Cypselas dorsiventrally flattened.* This is a traditional character of the *Cotula* group.

117 *Cypselas laterally winged.* Winged fruits occur also within the *Cotula* group, clade Ma17.

Leucoptera

1 reversed. See clade Ma5.

2 *Plants shrubby.* Several other genera in the *Cotula* group, as well as *Pentzia* and related genera, are also more or less shrubby.

Adenoglossa

15 reversed. *Leaves not variously deeply lobed or divided, but entire.*

25 *Leaves rather fleshy, entire, linear.*

52 reversed. *Ray floret limb not white, but yellow.*

75 reversed. See clade Ma14.

76 *Disc corolla zygomorphic with 2 smaller adaxial lobes with marginal resin canals extending from the base of the corolla and with 3 larger abaxial lobes.*

94 *Anthers with an apical resin sac.*

Clade Ma17 – The *Cotula* group of genera

72 *Disc corolla 4-lobed.* Some *Cotula* and *Soliva* species have 3-lobed corollas, another step in the reduction of the basically 5-lobed corolla. *Hippia* and *Eriocephalus* have 5-lobed corollas and the character is thus assumed to be reversed in these two genera. *Oncosiphon* also has 4-lobed corollas.

130 *Cypselas with 2 lateral vascular strands, sometimes also with 1 adaxial strand.*

172 *Pappus absent in ray and disc cypselas.*

177 *Chromosome number x=10.* A variety of chromosome numbers are known from *Cotula* but 10 appears to be the base number. Most of the related genera are not investigated karyologically but *Hilliardia* also has x=10. *Eriocephalus*, however, has x=9, the plesiomorphic base number of the tribe.

183 *Dehydrofalcarinone and dehydrofalcarinol present.* Most of the related genera have not been investigated chemically. However, these substances have been found also in *Tripleurospermum*. See further comments under that genus.

Hilliardia

2 *Plants shrubby.*

51 reversed. *Floral parts without resin canals.*

111 *Cypselas subglobose, with 2–3 very thin lateral-adaxial ribs.*

155 *Cypsela wall very thin, translucent and showing brownish black, rounded, very thick-walled testa epidermis cells.*

Clade Ma18

114 *Cypselas dorsiventrally flattened.*

Clade Ma19

117 *Cypselas laterally winged.*

133 *Cypselas with costal resin canals or sacs.*

Note: Leptinella and *Soliva* probably have their sister group(s) within *Cotula* as discussed under these genera. This is based on information other than that used to construct the cladogram. Thus *Cotula* could be paraphyletic and the characters appearing for *Cotula* in the cladogram should rather be interpreted as defining this clade, including all three genera, with reversals in *Leptinella* and *Soliva*.

Cotula

62 *Outer florets stalked.* This peculiar receptacular structure is a classical character for *Cotula*, though not particularly well developed in some species. Quite clearly it occurs also in *Schistostephium* and it is tempting to assume that it is a character for clade Ma18 although secondarily lost in the other genera of that clade. With this cladogram it is more parsimoniously interpreted as a parallelism between the two genera, however.

Clade Ma20

104 *Disc floret style-branches fused.* The same character occurs in *Hippia* and *Eriocephalus*.

Leptinella

70 *Corolla inflated with a hollow space between outer surface and inner layer.*

Soliva

1 *Plants annual.* Many species of *Cotula* are also annuals.

34 *Capitula sessile along the stems.*

36 *Capitula disciform.* Most species of *Cotula* as well as *Hippia* and *Schistostephium* are also disciform and it may be that the character is a synapomorphy for these genera. It is in conflict with other characters, however, and the presence of plesiomorphic, radiate species of *Cotula*, as well as the inclusion of *Eriocephalus* in clade Ma18, makes interpretation difficult.

63 *Outer female florets in several rows.* This character also occurs within *Cotula*, possibly indicating the sister group of *Soliva* within *Cotula*. See note under clade Ma19.

67 *Outer female florets without corollas.*

101 *Style persistent and spinescent in fruit.*

133 reversed. See clade Ma19.

Clade Ma21

2 *Plants shrubby.*

29 *Capitula densely corymbose.*

51 reversed. *Floral parts without resin canals.*

177 reversed. See clade Ma17.

Schistostephium

36 *Capitula disciform.* See comment under *Soliva*. Some *Schistostephium* species are discoid, here considered a further development from the disciform condition.

62 *Outer florets stalked.* See comment under *Cotula*.

Clade Ma22

72 reversed. See clade Ma17.

104 *Disc floret style-branches fused.*

Hippia

36 *Capitula disciform.* See comment under *Soliva*.

117 *Cypselas laterally winged.*

Eriocephalus

40 *Involucral bracts in 2 unequal series.*

45 *Receptacle paleate.*

50 *Receptacular paleae pilose.*

84. **CYMBOPAPPUS** B. Nord. in *Bot. Notiser* **129:** 150 (1976). Type species: *C. lasiopodus* (Hutch.) B. Nord. (*C. piliferus* (Thell.) B. Nord.).

Shrubs or half-shrubs. Leaves alternate, variously lobed or dentate, more or less ericoid. Capitula solitary, pedunculate, radiate. Receptacle convex to hemispherical or subconical, epaleate. Ray florets female, fertile; limb white or pinkish. Disc corolla 5-lobed; tube swollen and with thick vascular strands. Cypselas 5-ribbed, with large 2-celled glands and with myxogenic cells mainly abaxially; ribs with thick vascular strands. Pappus an oblique, adaxially longer whitish corona or cup, or of one large adaxial and one smaller abaxial scale.

DISTRIBUTION. S. Africa in the Cape, Transkei, and Transvaal. – 4 spp.

Cymbopappus based on species formerly classified as *Chrysanthemum* and *Marasmodes* (Nordenstam, 1976) is close to *Pentzia*. They are distinguished by *Cymbopappus* being radiate and *Pentzia* discoid. Hence the species of *Cymbopappus* have not been usually associated with *Pentzia* although Nordenstam (1976) noted the relationship. *Cymbopappus* also has an almost tubular pappus but a similar pappus occurs in species of *Pentzia*. The distinction between these two genera deserves further study.

C. adenosolen (Harvey) B. Nord.
C. hilliardiae B. Nord.
C. piliferus (Thell.) B. Nord.
C. lasiopodus (Hutch.) B. Nord.

85. **PENTZIA** Thunb. in *Prodr. pl. cap.*: 145 (1800). Type species: *P. crenata* Thunb. (*P. dentata* (L.) OK.).

Shrubs. Leaves alternate, variously pinnatisect, occasionally entire or apically dentate, more or less ericoid. Capitula solitary or corymbose, pedunculate, discoid. Receptacle convex or hemispherical to conical, epaleate. Corolla 5-lobed; tube generally swollen and with thick vascular strands. Cypselas 5-ribbed, often with large 2-celled glands and with myxogenic cells abaxially and on the ribs; ribs with thick vascular strands. Pappus an adaxial auricle, or an oblique adaxially longer cup, or of free adaxially longer whitish scales, sometimes absent.

DISTRIBUTION. S. Africa mainly in the Cape, also in Namibia, two species (*P. hesperidum* and *P. monodiana*) also in N. Africa in Morocco and Algeria. – 23 spp.

Traditionally (sensu Hutchinson, 1916*a*,*b*) *Pentzia* was all South African discoid Anthemideae with pinnatisect leaves and an epaleate receptacle. Two North African, typical *Pentzia* species, have also been described. Källersjö (1988) has recently re-classified *Pentzia* and most South African species included in *Tripleurospermum* have been assigned to a number of genera, including *Pentzia*, *Oncosiphon*, *Myxopappus* and *Foveolina*. *Pentzia* now comprises discoid shrubs (no annuals) with more or less ericoid leaves and 5-ribbed, myxogenic cypselas.

The separation of *Pentzia* from the small genera *Cymbopappus* and *Marasmodes* is problematical. In future it might turn out that the latter genera have their sister group within a presently paraphyletic *Pentzia*.

Clearly the generic delimitation of *Pentzia* is in need of detailed investigation, even after the removal of the annuals, as was undertaken by Källersjö.

At the species level *Pentzia* is also in need of revision. Some of the 'species' in the list below are probably conspecific but the list is taken from Källersjö (1986). References are also given to species described after Hutchinson's (1916*a*,*b*) revision since they were not included in his key.

P. argentea Hutch.
P. bolusii Hutch.
P. calcarea Kies – *Note:* Description in Kies, 1945.

P. calva S. Moore
P. cooperi Harvey
P. dentata (L.) OK.
P. elegans DC.
P. globosa Less.
P. hesperidum Maire & Wilczek – *Note:* Description in Maire, 1936.
P. incana (Thunb.) OK.
P. lanata Hutch.
P. monocephala S. Moore
P. monodiana Maire & Wilczek – *Note:* Description in Maire, 1929.
P. nana Burch.
P. pedunculariis B. Nord. – Note: Description in Nordenstam, 1987.
P. pinnatisecta Hutch.
P. punctata Harvey
P. quinquefida (Thunb.) Less.
P. sphaerocephala DC.
P. spinescens Less.
P. tomentosa B. Nord. – *Note:* Description in Nordenstam, 1967.
P. tortuosa (DC.) Fenzl ex Harvey
P. viridis Kies – *Note:* Description in Kies, 1945.

86. **MARASMODES** DC., *Prodr.* **6:** 136 (1838). Type species: *M. polycephalus* DC.

Shrubs. Leaves alternate, entire or occasionally lobed, linear, small, ericoid. Capitula small, closely aggregated at the stems, rarely solitary, discoid. Receptacle epaleate. Corolla 5-lobed, glandular; tube swollen and with thick vascular strands. Anthers short and comparatively wide. Cypselas 5-ribbed, glandular, with myxogenic cells mainly abaxially; ribs with thick vascular strands. Pappus of 7–10, oblong, flat, whitish, adaxially longer scales.

DISTRIBUTION. S. Africa in the Cape. – 4 spp.

Marasmodes is a genus of ericoid shrubs characterized by small and few-flowered, aggregated and sessile capitula and a pappus of several, whitish scales. *Pentzia* generally has larger, pedunculate capitula and a coroniform/auriculate pappus, only rarely of a few separate scales. Otherwise *Marasmodes* is very similar to many species of *Pentzia* and it seems clear that *Marasmodes* has its sister group within *Pentzia*. In *P. dentata* the capitula are small and arranged in groups and the pappus is more or less cleft approaching the condition in *Marasmodes*. *Adenosolen tenuifolius* from eastern Cape and described by de Candolle (1837) was tentatively retained by Harvey (1865), although he considered it very similar in habit to his *Marasmodes adenosolen* (*Cymbopappus adenosolen*) from south-western Cape. The genus *Adenosolen* was reduced by later authors to a synonym of *Marasmodes*. However, it appears that *Adenosolen tenuifolius* is neither a *Marasmodes* nor a *Cymbopappus*, since according to the description it has cypselas without a pappus. The matter requires further investigation.

Marasmodes was revised by Hutchinson (1917) but his key to the species cannot be recommended. The distinction between *M. oligocephalus* and *M. polycephalus* is better explained by Harvey (1865). *M. adenosolen* Harvey is *Cymbopappus adenosolen* (Harvey) B. Nord. Hutchinson did not see the type, and erroneously accepted the identification of another collection (*Schlechter* 7899) as *M. adenosolen*. That collection represents *M. oligocephalus*.

M. dummeri Bolus ex Hutch.
M. oligocephalus DC.
M. polycephalus DC.
M. undulata Compton – *Note:* Description in Compton, 1946.

87. **RENNERA** Merxm. in *Mitt. bot. StSamml. Münch.* **2**: 335 (1957). Type species: *R. limnophila* Merxm.

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, discoid. Receptacle hemispherical, epaleate. Corolla 5-lobed, with a narrow tube and a wide enervate limb; lobes with dorsal appendages. Cypselas obovoid or 5-angled, thick-walled and conspicuously tuberculate to rugose, apically sometimes with a thick, spreading to revolute rim. True pappus absent.

DISTRIBUTION. S. Africa in Namibia. – 3 spp.

Rennera is characterized by the specialized, thick-walled cypselas. The thick apical rim, called a 'pappus' by Merxmüller (1957), is present only in the type species. It does not seem to be homologous with the scarious pappus of *Pentzia* and many other Anthemideae. The thick spongy cypsela walls are presumably a dispersal adaptation; *R. limnophila* grows on temporarily submerged flats ('pans' and 'vleis'). Two of the species were recently transferred to *Rennera* from *Pentzia* by Källersjö (1988).

The position of *Rennera* is unclear. It is not necessarily closely related to *Pentzia* (as circumscribed here), but provisionally placed in the same subtribe, Matricariinae. In the cladogram (Fig. 12) it is grouped with other annual genera from the Mediterranean and South Africa. The position as sister group to *Oncosiphon* is debatable, however.

R. eenii (S. Moore) Källersjö (*Pentzia eenii* S. Moore)
R. limnophila Merxm.
R. laxa (Bremek. & Oberm.) Källersjö (*Pentzia laxa* Bremek. & Oberm.)

88. **ONCOSIPHON** Källersjö in *Bot. J. Linn. Soc.* **96**:310 (1988). Type species: *O. piluliferum* (L. f.) Källersjö.

Annual herbs. Leaves alternate, variously pinnatisect. Capitula solitary or corymbose, pedunculate, radiate or discoid. Receptacle flat to convex or conical to subglobose, epaleate. Ray florets female, fertile; limb white. Disc corolla 4-lobed; with a very much swollen and brittle tube and a campanulate, partly enervate limb; lobes with dorsal appendages. Cypselas 4-ribbed, without myxogenic cells, with a mainly abaxial entire or toothed rim. Pappus absent.

DISTRIBUTION. S. Africa mainly in the Cape, also in Namibia. – 8 spp.

The species of this genus were formerly classified in *Pentzia* and *Tripleurospermum*. The position of the genus is difficult to assess. It may be related to other annual genera of subtribe Matricariinae, where it is provisionally placed. A relationship to some other part of Anthemideae is not evident. The swollen corolla tube and absence of pappus is characteristic also of subtribe Achilleinae, but *Oncosiphon* is different at

least by its epaleate receptacle. The unusual chromosome numbers 2n=12 and 2n=16 (Nordenstam 1967, 1969; Mitsuoka & Ehrendorfer, 1972) are reported from species of this genus.

O. africanum (P. Bergius) Källersjö (*Matricaria capensis* L., *Matricaria hirta* (Thunb.) DC.)
O. glabratum (Thunb.) Källersjö
O. grandiflorum (Thunb.) Källersjö
O. intermedium (Hutch.) Källersjö
O. piluliferum (L. f.) Källersjö (*Matricaria globifera* (Thunb.) Fenzl ex Harvey, *Pentzia globifera* (Thunb.) Hutch.)
O. sabulosum (Wolley-Dod) Källersjö
O. schlechteri (Bolus) Källersjö
O. suffruticosum (L.) Källersjö (*Matricaria multiflora* Fenzl ex Harvey, *Pentzia tanacetifolia* (L.) Hutch.)

89. **OTOSPERMUM** Willk. in *Bot. Ztg* **22:** 251 (1864). Type species: *O. glabrum* (Lagasca) Willk.

An annual herb. Leaves alternate, pinnatisect. Capitula solitary or laxly corymbose, pedunculate, radiate. Receptacle conical, epaleate. Ray florets female, fertile; limb white; cypselas curved, basally connate to inner involucral bracts, with 1 abaxial and 2 lateral very thick ribs and 2–3 adaxial ribs, with myxogenic cells on the ribs; pappus an adaxial stiff auricle. Disc corolla 5-lobed; lobes with appendages; cypselas slightly curved, with 1 abaxial and 2 lateral thick ribs and 2 adaxial ribs, with myxogenic cells on the ribs; testa of thick-walled, much elongated and spirally arranged cells; pappus an adaxial stiff auricle, shorter than in ray cypselas.

DISTRIBUTION. SW Europe in Spain and Portugal, N. Africa in Morocco, Algeria, and Tunisia. – Monotypic.

The cypselas of *Otospermum* are unique in the Anthemideae. The three strong ribs are abaxially and laterally oriented, not adaxially and laterally as in *Matricaria* and some other genera. Nevertheless *Otospermum* seems best placed together with the other annual genera of Matricariinae.

90. **HETEROMERA** Pomel, *Nouv. mat. fl. atl.*: 60 (1874). Type species: *H. fuscata* (Desf.) Pomel.

An annual herb. Leaves alternate, pinnatisect. Capitula solitary, rather long-pedunculate, radiate. Receptacle convex, epaleate. Ray florets female; limb white, many-veined; cypselas dorsiventrally flattened, with 3 adaxial ribs with 1–3 resin canals; pappus a large adaxially longer scarious corona. Disc corolla 5-lobed; lobes with appendages; cypselas 5-ribbed with 1 adaxial and 2 lateral stronger ribs and 2 abaxial weaker ribs and with 3–5 resin sacs apically in the ribs, abaxially and on the ribs covered with myxogenic cells; pappus of 7–10 obovate, rounded, whitish, abaxially smaller scales.

DISTRIBUTION. N. Africa in Algeria, Tunisia and Libya. – Monotypic.

Heteromera fuscata, often known as *Chrysanthemum fuscatum* Desf., has sometimes been associated with two species known as *Chrysanthemum deserticola* (Murb.) F. Buxbaum and *Chrysanthemum trifurcatum* Desf. These have vallecular resin canals, however, and are here transferred to *Chrysanthoglossum* (Leucantheminae).

Heteromera fuscata has resin sacs in the ribs as in *Aaronsohnia*, *Matricaria*, *Daveaua*, and related genera. *Daveaua* appears to be the sister group. Both genera have the same kind of specialized ray cypselas, different from the disc cypselas. Alavi (1988) has used an eclectic treatment of the Matricariinae similar to that of Schultz Bipontinus (1860). In his treatment *Heteromera* is included in *Tripleurospermum*.

H. philaenorum Maire & Weller, which is more pubescent than the type species and has connate pappus scales, is probably a synonym of *H. fuscata* (Jeffrey, 1979*b*).

91. **DAVEAUA** Willk. ex Mariz in *Bolm Soc. broteriana* **9:** 243 (1891). Type species: *D. anthemoides* Mariz.

An annual herb. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Receptacle conical, epaleate. Ray florets female; limb white; cypselas dorsiventrally flattened, with 3 adaxial ribs, laterally winged; wings projected to apical teeth; pappus a large adaxial auricle. Disc corolla 5-lobed; tube basally swollen; lobes with appendages; cypselas 5-ribbed with 3–5 resin sacs apically in the ribs and with myxogenic cells; pappus absent.

DISTRIBUTION. SW Europe in Portugal and N. Africa in Morocco. – Monotypic.

Daveaua is apparently the sister group of *Heteromera*, both with the same kind of specialized ray cypselas.

The shape of the cypsela resin sacs is interesting, being intermediate between the elongated canals of *Aaronsohnia*, *Matricaria* and *Heteromera* and the rounded sacs of *Lonas* and *Tripleurospermum*, indicating the homology of these structures.

92. **MATRICARIA** L., *Sp. pl.*: 891 (1753). Type species: *M. recutita* L. (*Matricaria chamomilla* L. (1755), non L. 1753 quae est *M. inodora* L. (1763), *Chamomilla* Gray).

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, more or less pedunculate, radiate or disciform. Receptacle conical to subulate, hollow, epaleate. Ray florets female, fertile, with or without a white limb. Disc corolla 4- or 5-lobed; tube swollen in fruit; lobes rarely with resin canals. Cypselas slightly dorsiventrally compressed, with 5 mainly adaxially arranged thin ribs sometimes with resin canals, abaxially and on the ribs covered with myxogenic cells. Pappus absent or a small corona or sometimes, especially in ray cypselas, an adaxial auricle.

DISTRIBUTION. N. hemisphere, widespread in Europe, Middle East, temperate Asia, N. Africa and N. America, some species (e.g. *M. recutita*) widespread as weeds also in the S. hemisphere. – 7 spp.

Matricaria has characteristic, adaxially 5-ribbed fruits, and is thus clearly distinct from *Tripleurospermum*, with which it has been confused both taxonomically and nomenclaturally (see Pobedimova, 1961; Jeffrey, 1979*a*; Xifreda, 1985; Kergeulen et al., 1987). The question of typification was initially taken up by Hylander (1945) who considered that the name *Matricaria chamomilla* L. should be retained, although the description had been applied to the species now known as *Tripleurospermum inodorum* (L.) Schultz-Bip. in Linnaeus's *Species plantarum* (1753). Similarly, Toman & Stary (1965)

argued for the retention of *Matricaria chamomilla* L. on the grounds that it had been widely used in pharmalocogical literature. The selection of the Hortus Cliffortianus Linnean specimen of *M. chamomilla* L. as the lectotype was made by Grierson in Davis (1975) on the grounds that the phrase name 'Matricaria foliis supra decompositis setaceis pedunculis solitariis' remained constant with the name *Matricaria chamomilla* L. in all of Linnaeus's works. However, the Hortus Cliffortianus specimen of *M. chamomilla* has coronate cypselas and does not therefore agree with Linnaeus's generic concept of *Matricaria*. The next choice of generic lectotypification, *Matricaria recutita* L., was made by Pobedimova, a species which agrees well with the generic description, because of its ecoronate cypselas (Jeffrey, 1979*a*) and therefore is utilized here.

The typification of *Matricaria* as based on *Chamomilla vulgaris* Gray was discussed by Rauschert (1974) who argued that *Matricaria* had been misapplied and must therefore be rejected. He argued that *Chamomilla* was the correct name for *Matricaria* and that *Matricaria* should be applied as the correct name for *Tripleurospermum* on the basis that *M. chamomilla* L. (1753) is equivalent to *M. perforata* Mérat. He accordingly made the relevant new combinations in *Tripleurospermum* and *Chamomilla*.

However, we reject Rauschert's argument since the typification of *M. chamomilla* L. (Grierson in Davis, 1975) and *M. recutita* L. are tied with the same generic concept. Indeed, Grierson considered that the two species were mere varieties of the same species. We accept Jeffrey's (1979*a*) argument that because the type species was clearly designated by Pobedimova (1961) there is no confusion as to the correct application of Linnaeus's *Matricaria* and indeed the occasional misapplication to *Tripleurospermum* has not involved either type. Hence, *M. recutita* L. is the type species of *Matricaria*.

Matricaria lasiocarpa Boiss. (*Chamomilla lasiocarpa* (Boiss.) Rauschert) is a species which we place in *Microcephala*. This genus has a number of autapomorphies not shared by *Matricaria*. *Matricaria* may be paraphyletic with *Microcephala* excluded.

Tanacetum ledebourii (Schultz-Bip.) Schischk. from central Asia, also known as *Matricaria songarica*, is transferred into *Matricaria*. Tzvelev in *Flora URSS* (Komarov, 1961) included it in a monotypic, annual section of *Cancrinia* as *C. discoidea*. However, it has fruits typical of *Matricaria* and also agrees with *Matricaria* in several other characters.

M. aurea (Loefl.) Schultz-Bip., (*Chamomilla aurea* (Loefl.) Gay ex Cosson & Kralik). Mediterranean, S. Europe, throughout N. Africa, the Middle East, and SW Asia to C. Asia.

**M. macrotis* Rech. f. (*Chamomilla macrotis* (Rech. f.) Rauschert). Turkey.

M. matricarioides Porter ex Britton (*M. discoidea* DC., *Chamomilla suaveolens* (Pursh) Rydb.). W. North America, widespread as a cosmopolitan weed.

M. occidentalis Greene (*Chamomilla occidentalis* (Greene) Rauschert). W. North America.

M. recutita (L.) Rauschert (*Matricaria chamomilla* L. (1755) non L. 1753 (= *Matricaria inodora* L., *Tripleurospermum inodorum* (L.) Schultz-Bip.). Throughout Europe and most of temperate Asia, widespread as a cosmopolitan weed.

M. songarica Bunge (*Tanacetum ledebourii* Schultz-Bip., *Pyrethrum discoideum* Ledeb.). C. Asia, Mongolia and China in Sinkiang.

**M. tzvelevii* Pobed. (*Chamomilla tzvelevii* (Pobed.) Rauschert). Krym.

93. **MICROCEPHALA** Pobed. in *Bot. Mater. Gerb. bot. Inst. V. A. Komarova* **21:** 356 (1961). Type species: *M. lamellata* (Bunge) Pobed.

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, rather long-pedunculate, radiate or discoid. Receptacle conical, hollow, epaleate. Ray florets female, fertile; limb white or pink. Disc corolla 5-lobed. Cypselas with 5 adaxially arranged ribs, abaxially and on the ribs with myxogenic cells, laterally with rather stiff, unbranched hairs of 3–8 cells with spiral cell wall thickenings; testa of much elongated spirally arranged cells. Pappus a large deeply fimbriate, whitish corona, in ray cypselas abaxially split to the base thus forming a large adaxial, deeply fimbriate auricle.

DISTRIBUTION. C. and middle Asia, Iran, Afghanistan Pakistan. – 4 spp.

Microcephala is well characterized by its peculiar cypsela hairs. The hair cells have spiral wall thickenings and are rather stiff. The five adaxially arranged cypsela ribs indicate a relationship with *Matricaria*. Apparently they are sister groups, or *Microcephala* may have its sister group within a paraphyletic *Matricaria*. In habit *Microcephala* is very similar to *Matricaria*.

M. afghanica Podl.

M. deserticola Podl.

M. lamellata (Bunge) Pobed. (*Chamomilla lasiocarpa* (Boiss.) Rauschert, *M. lasiocarpa* (Boiss.) Pobed., *M. turcomanica* (Winkler) Pobed.).

M. subglobosa (H. Kraschen.) Pobed.

94. **ENDOPAPPUS** Schultz-Bip. in *Bonplandia, Hannover* **8:** 369 (1860). Type species: *E. macrocarpus* Schultz-Bip.

An annual herb. Leaves alternate, pinnatisect. Capitula solitary, rather long-pedunculate, radiate. Involucral bracts with wide scarious margins. Receptacle flat, epaleate. Ray florets female, fertile; limb white or yellow, many-veined. Disc corolla 5-lobed. Cypselas comparatively large, with 1 adaxial and 2 lateral thick sclerenchymatous and much protruding ribs, in ray cypselas somewhat winged, abaxially and on the ribs and pappus with myxogenic cells. Pappus a stiff short corona.

DISTRIBUTION. N. Africa in Morocco, Algeria and Tunisia. – Monotypic.

Endopappus has no obvious close relatives but the cypsela shape with three adaxially and laterally thick ribs is similar to that of *Tripleurospermum*. *Endopappus* has no cypsela resin sacs, however. Nevertheless it is perhaps best considered together with *Tripleurospermum*. The South African *Myxopappus* and *Foveolina* are also possible relatives.

The species is sometimes known as *Chrysanthemum macrocarpum* Cosson & Kralik or *Pyrethrum macrocarpum* (Cosson & Kralik) Alavi.

95. **MYXOPAPPUS** Källersjö in *Bot. J. Linn. Soc.* **96:** 314 (1988). Type species: *M. acutilobus* (DC.) Källersjö.

Annual herbs. Leaves alternate, variously pinnatisect. Capitula solitary, pedunculate, discoid. Involucral bracts almost subulate, without scarious margins. Receptacle convex to conical, epaleate. Disc corolla 4- or 5-lobed. Cypselas with 1 adaxial and 2 lateral thick ribs, with myxogenic cells abaxially and on the ribs; cypsela wall white, spongy and containing numerous druses. Pappus an apical corona, covered with myxogenic cells.

DISTRIBUTION. S. Africa in the Cape, Namibia. – 2 spp.

The two species of *Myxopappus* were recently removed from *Pentzia* by Källersjö. They seem related to *Foveolina*, another genus described by Källersjö. Both *Myxopappus* and *Foveolina* have fruits similar to those of *Tripleurospermum* and *Endopappus*, and are hence grouped together with them in subtribe Matricariinae. The unusual chromosome number 2n=14 was reported by Nordenstam (1967).

M. acutilobus (DC.) Källersjö
M. hereroensis (O. Hoffm.) Källersjö (*Pentzia galpinii* Hutch.)

96. **FOVEOLINA** Källersjö in *Bot. J. Linn. Soc.* **96:** 316 (1988). Type species: *F. dichotoma* (DC.) Källersjö.

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate, disciform or discoid. Receptacle flat to convex to conical, epaleate. Ray florets female, fertile; limb white; cypselas adaxially somewhat flattened and inconspicuously 3-ribbed, abaxially rounded and covered with myxogenic cells; cypsela wall adaxially white and spongy with numerous druses, abaxially very thin and transparent; pappus white and spongy, an adaxial auricle or occasionally coroniform. If disciform, outer female florets filiform with cypselas almost terete, without myxogenic cells and without pappus; cypsela wall spongy and conspicuously wrinkled. Central florets with corolla 4- or 5-lobed; tube often basally dilated or saccate; cypselas either as in ray florets and with a pappus, or obovoid with a very thin cypsela wall all around and without a pappus, always abaxially with myxogenic cells.

DISTRIBUTION. S. Africa in the Cape, Namibia. – 5 spp.

Foveolina comprises species formerly in *Pentzia* and '*Matricaria*'. The genus is related to *Myxopappus*, *Tripleurospermum* and other genera in subtribe Matricariinae. Two of the species, *F. albidiformis* and *F. schinziana*, are somewhat aberrant and resemble species of *Cotula*. The matter is discussed in detail by Källersjö (1988).

F. albida (DC.) Källersjö (*Pentzia annua* DC.)
F. albidiformis (Thell.) Källersjö (*Pentzia membranacea* Hutch.)
F. dichotoma (DC.) Källersjö
F. schinziana (Thell.) Källersjö
F. tenella (DC.) Källersjö

97. **LONAS** Adans., *Fam. pl.* **2**: 118 (1763). Type species: *Santolina annua* L. (*L. annua* (L.) Vines & Druce).

A glabrous annual herb. Leaves alternate, pinnatisect. Capitula in pedunculate dense corymbs, discoid. Receptacle elongated, paleate; paleae somewhat canaliculate, with a central resin canal. Corolla 5-lobed. Cypselas with 1 adaxial and 2 lateral vascular strands and ribs, with a single resin sac apically in the adaxial rib, abaxially and on the ribs covered with myxogenic cells. Pappus a scarious fimbriate corona.

DISTRIBUTION. Mediterranean, S. Europe in Italy and N. Africa in Morocco, Algeria, and Tunisia. – Monotypic.

The position of *Lonas* is difficult to assess but we have placed it in the Matricariinae together with *Tripleurospermum* and related genera because of their similar fruits. *Lonas* differs by its densely corymbose capitula and by its paleate receptacle, both uncommon characters in Matricariinae. However, the arrangement of the myxogenic cells on the cypselas is typical of this subtribe.

98. **TRIPLEUROSPERMUM** Schultz-Bip., *Tanaceteen*: 31–34 (1844*a*). Type species: *Tripleurospermum inodorum* Schultz-Bip.

Annual or perennial herbs. Leaves alternate, pinnatisect. Capitula solitary or corymbose, pedunculate, radiate, disciform or discoid. Receptacle convex to conical, epaleate. Ray florets female; limb white or rarely pale pink. Disc corolla 5-lobed; lobes each usually with a resin sac. Cypselas triquetrous with 1 adaxial and 2 lateral usually thick whitish ribs and sometimes 1–2 abaxial thin ribs, often rugose or tuberculate abaxially and between the ribs, sometimes with myxogenic cells, abaxially and apically with 2 distinct, occasionally 1 or 3–5, resin sacs. Pappus a corona or auricle, or of few scales, sometimes absent. Embryo sac tetrasporic. Flavonol 7-glycosides and dehydrofalcarinone and dehydrofalcarinol present.

DISTRIBUTION. Europe and temperate Asia, a few species also in N. America (*T. maritimum* and *T. perforatum* naturalized) and N. Africa (*T. auriculatum*), one species (*T. perforatum*) widespread as a weed; most species in SE Europe and SW Asia. – 38 spp.

Despite the comparatively large number of species, *Tripleurospermum* as presently circumscribed is a distinct genus with characteristic 3-ribbed cypselas with 2 abaxial-apical resin sacs. Chemically about 30 species have been investigated for flavonol glycosides and they all contain 7-glycosides rather than the common 3-glycosides as, for example, in *Matricaria* (Greger, 1975, 1977). Species of *Tripleurospermum* embryologically investigated have a tetrasporic embryo sac.

In habit *Tripleurospermum* is similar to many other Anthemideae. The genus was earlier more widely and less distinctly circumscribed, so as to also include *Matricaria*. However, we keep the genus distinct following Pobedimova in *Flora USSR* (Komarov, 1961) and Grierson in *Flora of Turkey* (Davis, 1975). *Tripleurospermum* as here understood follows the original concept of Schultz Bipontinus (1844*a*). The South African species described under *Matricaria* are now transferred to other genera (Källersjö, 1988).

As described under *Matricaria* Rauschert (1974) and Kay (1976) missapplied the name *Matricaria* to refer exclusively to

the species of *Tripleurospermum*. Because Rauschert (1974) transferred a number of species from *Tripleurospermum* to *Matricaria* we have cited a more complete synonomy. The species list is compiled from the standard floras with later species and species described from other areas added, for example E. Hossain in *Flora of Turkey* (Davis, 1975).

T. auriculatum (Boiss.) Rech. fil. (*Matricaria auriculata* (Boiss.) Ball). Middle East.
T. baytopianum E. Hossain. Turkey.
T. breviradiatum (Ledeb.) Pobed. (*Matricaria breviradiata* (Ledeb.) Rauschert). W. Siberia.
T. callosum (Boiss. & Heldr.) E. Hossain (*Chamaemelum callosum* Boiss. & Heldr.). Turkey.
T. caucasicum (Willd.) Hayek (*Matricaria caucasica* (Willd.) Poiret). SE Europe, Turkey, Caucasus, Middle East, Iraq, Iran, Afghanistan.
T. colchicum (Manden.) Pobed. (*Matricaria colchica* (Manden.) Rauschert). Caucasus.
**T. conoclinium* (Boiss. & Balansa) Hayek (*Matricaria conoclinia* (Boiss. & Balansa) Nyman). Turkey.
**T. corymbosum* E. Hossain (non *Matricaria corymbosa* Desr. in Lam.). Turkey.
T. daghestanicum (Rupr. ex Boiss.) Bremer & Humphries, **comb. nov**. Basionym: *Chamaemelum daghestanicum* Rupr. ex Boiss., *Fl. orient.* **3**: 334 (1875) (*Matricaria daghestanica* (Rupr. ex Boiss.) Rauschert).
T. decipiens (Fischer & C. Meyer) Bornm. (*Matricaria decipiens* (Fischer & C. Meyer) K. Koch). Turkey, Caucasus, Iran.
T. disciforme (C. Meyer) Schultz-Bip. (*Matricaria disciformis* (C. Meyer) DC.). Turkey, Caucasus, Iraq, Iran, Afghanistan, Pakistan, C. Asia.
**T. elongatum* (Fischer & C. Meyer ex DC.) Bornm. (*Matricaria elongata* (Fischer & C. Meyer ex DC.) Hand.-Mazz., *M. australis* (Pobed.) Rauschert, *Tripleurospermum australe* Pobed.). Turkey, Caucasus. – *Note: T. australe* was included as a doubtful synonym by E. Hossain in *Flora of Turkey* (Davis, 1975).
**T. fissurale* (Sosn.) E. Hossain. Turkey.
**T. froedinii* Rech. f. (*Matricaria froedinii* (Rech. f.) Rauschert). Iran.
**T. grossheimii* (Fed.) Pobed. (*Matricaria grossheimii* (Fed.) Rauschert). Caucasus.
T. heterolepis (Freyn & Sint.) Bornm. (*Chamaemelum heterolepis* Freyn & Sint.). Turkey.
**T. homogamum* G. X. Fu. China.
T. hygrophilum (Bornm.) Bornm. (*Matricaria hygrophila* (Bornm.) Rauschert). Turkey.
T. karjaginii (Manden. & Sof.) Pobed. (*Matricaria karjaginii* (Manden. & Sof.) Rauschert). Caucasus.
T. kotschyi (Boiss.) E. Hossain (*Chamaemelum kotschyi* Boiss.). Turkey.
T. limosum (Maxim.) Pobed. (*Matricaria limosa* (Maxim.) Kudo). Far East, Japan, China.
T. maritimum (L.) K. Koch (*Matricaria maritimum* L. *Tripleurospermum ambiguum* (Ledeb.) Franchet & Savat., *T. phaeocephalum* (Rupr.) Pobed., *T. subpolare* Pobed.). Throughout most of Europe, temperate Asia and in North America. – *Note:* in *Flora europaea* three subspecies are recognized: ssp. *maritimum*, ssp. *phaeocephalum* (Rupr.) Rauschert, and ssp. *subpolare* (Pobed.) Rauschert. The related weedy species *T. perforatum* (= *T. inodorum*) has been kept separate.
T. microcephalum (Boiss.) Bornm. (non *Matricaria microcephala* C. Koch, *M. armeniaca* Rauschert). Turkey, Iran, Iraq.
T. monticolum (Boiss. & Huet) Bornm. (*Matricaria monticola* (Boiss. & Huet) Rauschert). Turkey.
T. oreades (Boiss.) Rech f. (*Matricaria oreades* Boiss., *Matricaria halepensis* Rauschert, *Matricaria szowitzii* (DC.) Rauschert, *Tripleurospermum szowitzii* (DC.) Pobed., *Matricaria tchihatchewii* (Boiss.) Voss, *Tripleurospermum tchihatchewii* (Boiss.) Bornm.). Turkey, Middle East, Caucasus, Iran. – *Note: Matricaria halepensis* was a new name for *Chamaemelum grandiflorum* Boiss. & Hausskn., the epithet of which is already occupied in *Matricaria*. However, this species as well as the others listed in the synonymy above were reduced by E. Hossain in *Flora of Turkey* (Davis, 1975).
T. parviflorum (Willd.) Podeb. (*Matricaria parviflora* (Willd.) Poiret). E. Europe in Russia, Turkey, Caucasus, Middle East, Iraq, Iran, Pakistan, C. Asia.
T. perforatum (Mérat) Lainz (*Matricaria perforata* Mérat, *Matricaria inodora* L., *Tripleurospermum inodorum* (L.) Schultz-Bip.). Throughout most of Europe and temperate Asia, widespread as a weed especially in North America etc. – *Note:* See *T. maritimum*.
**T. pichleri* (Boiss.) Bornm. (*Matricaria pichleri* (Boiss.) Rauschert). Turkey.
T. repens (Freyn & Sint.) Bornm. Turkey.
T. rosellum (Boiss. & Orph.) Hayek (*Matricaria rosella* (Boiss. & Orph.) Nyman, *Matricaria lesbiaca* (Candargy) Rauschert, *Tripleurospermum lesbiacum* (Candargy) Rech. f.). SE Europe in Greece, Turkey. – *Note:* The synonymous names are from E. Hossain in *Flora of Turkey* (Davis, 1975).
**T. rupestre* (Sommier & Levier) Pobed. (*Matricaria rupestris* (Sommier & Levier) Rauschert). Caucasus.
T. sevanense (Manden.) Pobed. (*Matricaria sevanensis* (Manden.) Rauschert). Turkey, Caucasus, Iran.
T. subnivale Pobed. (*Matricaria subnivalis* (Pobed.) Rauschert). Caucasus.
T. tempskyanum (Freyn & Sint.) Hayek (*Matricaria tempskyana* (Freyn & Sint.) Rauschert). SE Europe in Greece.
T. tenuifolium (Kit.) Freyn (*Matricaria trichophylla* (Boiss.) Boiss.). SE and C. Europe, Turkey.
T. tetragonospermum (Schum.) Pobed. (*Matricaria tetragonosperma* (Schum.) Hara & Kitam.). W. Siberia, Far East, Japan, China.
T. transcaucasicum (Manden.) Pobed. (*Matricaria transcaucasica* (Manden.) Rauschert). Turkey, Caucasus.
**T. tzvelevii* Pobed. (non *Matricaria tzvelevii* Pobed.), (*M. aserbaidshanica* Rauschert). Caucasus.

99. **AARONSOHNIA** Warb. & Eig in *Bull. agric. Exp. Stn, Tel-Aviv* **6**: 39 (1927). Type species: *A. factorovskyi* Warb. & Eig.

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, rather long-pedunculate, radiate, disciform, or discoid. Receptacle conical, epaleate. Ray florets female, fertile, with or without a white limb. Disc corolla 5-lobed; tube basally and especially abaxially much swollen in fruit; lobes with central resin canals. Cypselas slightly dorsiventrally flattened with 1 adaxial and 2 lateral vascular strands and often with 2 lateral resin canals, abaxially covered with myxogenic cells.

Pappus an adaxial, conspicuous, whitish auricle, sometimes absent.

DISTRIBUTION. Middle East and N. Africa in Morocco, Algeria, Tunisia and Libya. – 2 spp.

During this study it became clear that *Chlamydophora pubescens* in almost all details agrees with the circumscription of the monotypic genus *Aaronsohnia* from the Middle East. Thus, we have transferred it to *Aaronsohnia*. *A. pubescens* is a sometimes radiate or discoid species from North Africa.

Aaronsohnia is similar to *Cotula* and other herbaceous members of the *Cotula* group. However, it is probably more closely related to *Matricaria*, *Leucoptera* and *Adenoglossa* as indicated by the character analysis.

A. factorovskyi Warb. & Eig

A. pubescens (Desf.) Bremer & Humphries, **comb. nov.** Basionym: *Cotula pubescens* Desf., *Fl. atlant.* **2:** 284 (1799) (*Chlamydophora pubescens* (Desf.) Cosson & Durieu, *Matricaria pubescens* (Desf.) Schultz-Bip., *Chamomilla pubescens* (Desf.) Alavi).

100. **LEUCOPTERA** B. Nord. in *Bot. Notiser* **129**: 141 (1976). Type species: *L. nodosa* (Thunb.) B. Nord.

Shrublets. Leaves alternate or opposite, entire or few-lobed, somewhat fleshy. Capitula solitary, long-pedunculate, radiate. Involucral bracts wide, many-veined. Receptacle convex, epaleate. Ray florets female, fertile; limb white, often becoming pink-reddish. Disc corolla 5-lobed; lobes generally with central resin sacs. Anthers with endothecial tissue mainly polarized. Cypselas dorsiventrally flattened, laterally winged, whitish, with 1 adaxial and 2 lateral vascular strands, generally with 2 lateral resin canals, abaxially covered with elongated apically projected myxogenic cells. Pappus of 1 larger adaxial auricle and 2 smaller adaxial-lateral scales.

DISTRIBUTION. S. Africa in the Cape. – 3 spp.

This distinct, recently described genus of three species is closely related to *Adenoglossa*. Indeed, they are sister groups as stated by Nordenstam (1976). He also considered *Leucoptera* monophyletic, despite the fact that it is plesiomorphic in most characters in comparison to *Adenoglossa*.

Leucoptera and *Adenoglossa* are similar to the *Cotula* group in fruit morphology. However, they are possibly more closely related to the northern hemisphere species of *Matricaria* and *Aaronsohnia* as indicated by the cladogram (Fig. 12). Their position within the Matricariinae is uncertain.

L. nodosa (Thunb.) B. Nord.
L. oppositifolia B. Nord.
L. subcarnosa B. Nord.

101. **ADENOGLOSSA** B. Nord. in *Bot. Notiser* **129:** 137 (1976). Type species: *A. decurrens* (Hutch.) B. Nord.

An annual herb. Leaves alternate or opposite, entire, fleshy. Capitula solitary, long-pedunculate, radiate. Involucral bracts wide, many-veined. Receptacle conical, epaleate. Ray florets female, fertile; limb short, yellow. Disc corolla 5-lobed, slightly zygomorphic with 2 smaller adaxial lobes with marginal resin canals extending from the base of the corolla and with 3 larger abaxial lobes. Anthers with an apical resin sac; endothecial tissue partly polarized. Cypselas dorsiventrally flattened, laterally winged, whitish, with 1 adaxial and 2 lateral vascular strands and with 2 lateral resin canals, abaxially covered with elongated apically projected myxogenic cells. Pappus of 1 larger adaxial auricle, 2 larger adaxial-lateral scales, and 2–3 smaller abaxial scales.

DISTRIBUTION. S. Africa in the NW Cape. – Monotypic.

Adenoglossa is a recently described monotypic genus with a number of autapomorphies. It is closely related to *Leucoptera* and their interrelationship is discussed under that genus.

102. **HILLIARDIA** B. Nord. in *Op. bot. Soc. bot. Lund* **92:** 147 (1987). Type species: *H. zuurbergensis* (Oliver) B. Nord.

A scrambling shrub. Leaves alternate, flat, pinnatisect. Capitula laxly corymbose, pedunculate, radiate. Receptacle conical to elongated, epaleate. Ray florets female, fertile; limb white, many-veined, apically rather deeply bifid. Disc corolla 4-lobed. Cypselas subglobose, with 2–3 very thin adaxial ribs; cypsela wall very thin, translucent and showing the brownish black, rounded and very thick-walled testa epidermis cells. Pappus absent.

DISTRIBUTION. S. Africa in the Cape and Natal. – Monotypic.

Hilliardia was formerly included in *Matricaria* but it is related neither to the northern hemisphere *Matricaria* s. s. nor to the South African *Matricaria* species transferred to various other genera (*Myxopappus*, *Foveolina*, *Oncosiphon*, *Cotula*). *Hilliardia* has unusual thin-walled fruits, with an extremely well developed testa (seen in mature fruits only). The shape and venation of the fruits recall *Achillea* and *Cotula*. *Hilliardia* is also similar to *Cotula* and its South African relatives have a 4-lobed corolla and a chromosome number of x=10, hence our placement of *Hilliardia* within the *Cotula* group.

103. **COTULA** L., *Sp. pl.*: 891 (1753). Type species: *C. coronopifolia* L. – *Brocchia* Vis., *Cenia* Comm. ex Juss., *Otochlamys* DC., *Sphaeroclinium* (DC.) Schultz-Bip.

Annual or perennial herbs. Leaves alternate or sometimes opposite or rosulate, pinnatisect, lobed or occasionally entire. Capitula solitary, pedunculate, generally disciform or discoid or rarely shortly radiate; peduncles sometimes inflated below the capitulum. Receptacle flat to conical, epaleate. Ray or outer female florets fertile, in one to several rows, generally stalked; tube short or absent; limb generally absent, white if present. Disc corolla 4-lobed, occasionally 3-lobed, abaxially sometimes saccate; lobes generally with central resin canals, one lobe occasionally expanded to a radiate limb. Cypselas dorsiventrally flattened, often laterally winged, with 2 lateral (occasionally 3 or 4) vascular strands and sometimes with 2 lateral resin canals, generally with blunt uniseriate hairs, sometimes with myxogenic cells. Pappus absent. Flavonol 5–glycosides and dehydrofalcarinone and dehydrofalcarinol present.

DISTRIBUTION. S. hemisphere, mainly in S. Africa, also in Australia, S. America (*C. mexicana*), and on the S. oceanic islands (*C. goughensis*, *C. moseleyi*), a few species extending

to E. Africa (*C. abyssinica*, *C. cryptocephala*), N. Africa (*C. cinerea*), and to Mexico (*C. mexicana*); a few widespread weedy species (*C. anthemoides*, *C. australis*, *C. coronopifolia*). – 55 spp.

Cotula is generally conceived as disciform or discoid, except for some South African species with rays secondarily evolved from one of the disc floret corolla lobes. But there is also a South African *C. montana* (Adamson et al., 1944) with true rays. It is clearly a *Cotula* with its typical fruits and stalked rays. Thus, it appears that *Cotula* may be radiate as well as disciform or discoid.

The monotypic genus *Sphaeroclinium*, revived by Mitsuoka & Ehrendorfer (1972), is included as a synonym of *Cotula*. The South African species, *S. nigellifolium*, was originally described as a species of *Matricaria*, a 'dustbin' genus in South Africa used for various species of unknown relationships. Since the species is radiate its close relationship to the generally disciform species of *Cotula* is not immediately obvious. Furthermore, the marginal florets, i. e. the rays, are not stalked in *Sphaeroclinium* as in most species of *Cotula*. However, there are several species of *Cotula* with very shortly stalked or sessile rays and there is at least one described radiate species *C. montana*. Thus, the distinction between *Sphaeroclinium* and *Cotula* disappears on closer examination. Both genera have a similar habit, 4-lobed corollas, the same specialized cypsela morphology, a chromosome number of x=10, and related chemistry.

Another South African species of '*Matricaria*' belonging here is *M. andreae* E. Phillips. It was described as a *Matricaria* presumably because it is radiate but the fruit morphology leaves no doubt about its generic position. Thus, it is recombined here as *Cotula andreae*.

Lloyd (1972*a*,*b*) recognized three sections within *Cotula*: sect. *Cotula* with usually one row of rays, sect. *Strongylosperma* with several rows of rays and sect. *Leptinella* with inflated corollas. Sect. *Leptinella* is recognized as a distinct genus (Lloyd & Webb, 1987) but the demarcation between the other two sections is difficult since they can hardly be defined as monophyletic groups. The South African segregate genera *Cenia*, with inflated peduncles, and *Otochlamys*, with an abaxially saccate corolla, are included in sect. *Cotula*. Most species belong to this section, which is mainly South African. Sect. *Cotula* together with sect. *Strongylosperma* are clearly in need of revision and the sectional delimitation should be reconsidered.

It is also possible that *Cotula* is paraphyletic with *Leptinella* and *Soliva* excluded. *Soliva* with several rows of ray florets is possibly derived from sect. *Strongylosperma* or part of it. In the cladogram *Leptinella* and *Soliva* are sister genera, united by their functionally male disc florets, but interrelationships between these two genera and the subunits of *Cotula* deserve further investigation.

Identification of *Cotula* species, especially South African, is difficult, since the genus is not revised and since the descriptions are scattered in the literature. In South Africa as a whole only *Flora capensis* (Harvey, 1865) is available and there are numerous species described later. References are given in the list of species. However, for Natal with its eight species there is a modern treatment by Hilliard (1977).

C. abyssinica Schultz-Bip. E. Africa.
C. alpina (Hook. f.) Hook. f. Australia.
C. andreae (E. Phillips) Bremer & Humphries, **comb. nov.** Basionym: *Matricaria andreae* E. Phillips in *Jl. S. Afr. Bot.* **16:** 21 (1950). S. Africa.
C. anthemoides L. S. Africa, widespread as a cosmopolitan weed.
C. australis (Sieber ex Sprengel) Hook. f. Australia, widespread as a cosmopolitan weed.
C. barbata DC. S. Africa.
C. bipinnata Thunb. S. Africa, naturalized in Australia.
**C. bracteolata* E. Meyer ex DC. S. Africa.
C. ceniifolia DC. S. Africa.
C. cinerea Del. (*Brocchia cinerea* (Del.) Vis.). N. Africa. – *Note:* This species seems aberrant within *Cotula*. It has been described as the genus *Brocchia*, which possibly should be re-established. The matter requires further study.
C. coronopifolia L. S. Africa, Australia, widespread as a cosmopolitan weed.
**C. cotuloides* (Steetz) Druce. Australia.
C. cryptocephala Schultz-Bip. ex A. Richard. E. Africa.
**C. dielsii* Muschler. S. Africa.
C. duckittiae (L. Bolus) Bremer & Humphries, **comb. nov.** Basionym: *Cenia duckittiae* L. Bolus in *Ann. Bolus Herb.* **4**: 15 (1925) (*Cenia expansa* Compton). S. Africa. – *Note: C. expansa* is provisionally included here as a synonym. We find it hardly distinct and hesitate to make a new combination unnecessarily.
C. eckloniana (DC.) Levyns (*Otochlamys eckloniana* DC.). S. Africa.
**C. elongata* Vogel. Java.
C. filifolia Thunb. S. Africa.
**C. goughensis* R. N. R. Brown. Gough Island.
C. heterocarpa DC. S. Africa.
C. hispida (DC.) Harvey. S. Africa.
C. laxa DC. S. Africa.
C. leptalea DC. S. Africa.
C. lineariloba (DC.) Hilliard. S. Africa.
**C. loganii* Hutch. S. Africa.
**C. macroglossa* Bolus ex Schltr. S. Africa.
C. mariae Bremer & Humphries, **nom. nov.** Basionym: *Cenia pectinata* DC., *Prodr.* **6**: 83 (1837) (non *Cotula pectinata* Hook. f.) – *Note:* We name this species after Ms. Mari Källersjö in recognition of her contributions to the classification of South African Anthemideae. S. Africa.
C. melaleuca Bolus. S. Africa.
C. membranifolia Hilliard. S. Africa.
C. mexicana (DC.) Cabrera (*C. pygmaea* Benth. in Benth. & Hook. f., *C. pedicellata* (Ruíz Lopez & Pavon) Cabrera (non Compton), *C. cabrerae* Caro). S. and C. America, Mexico.
C. microglossa (DC.) O. Hoffm. & Kunze ex Kunze. (*Cenia albovillosa* S. Moore, *Cenia microglossa* DC.) – *Note: C. albovillosa* is provisionally included as a synonym. We find it hardly distinct and hesitate to make a new combination unnecessarily. S. Africa.
C. montana Compton. S. Africa.
C. moseleyi Hemsley. Tristan d'Acuna.
C. myriophylloides Harvey in Hook. S. Africa.
C. nigellifolia (DC.) Bremer & Humphries, **comb. nov.** Basionym: *Matricaria nigellifolia* DC., *Prodr.* **6**: 50 (1837) (*Sphaeroclinium nigellifolium* (DC.) Schultz-Bip.). S. Africa.
C. nudicaulis Thunb. S. Africa.
C. paludosa Hilliard. S. Africa.
**C. paradoxa* Schinz. S. Africa.

**C. pedicellata* Compton. S. Africa.
C. pedunculata (Schltr) E. Phillips (*Otochlamys pedunculata* Schltr. S. Africa.
**C. pterocarpa* DC. S. Africa.
C. pusilla Thunb. S. Africa.
**C. radiata* O. Hoffm. ex OK. S. Africa.
C. radicalis (Killick & Claassen) Hilliard & Burtt. S. Africa.
**C. rosea* Boj. ex Less. Madagascar.
C. sericea L. f. (*Cenia sericea* (L. f.) DC.). S. Africa.
C. socialis Hilliard. S. Africa.
C. sororia DC. S. Africa.
**C. stenophylla* K. Koch. S. Africa.
C. tenella E. Meyer ex DC. S. Africa.
C. thunbergii Harvey. S. Africa.
C. turbinata L. (*Cenia turbinata* (L.) Pers.). S. Africa, naturalized in Australia.
C. villosa DC. (*C. multifida* DC.). S. Africa.
C. vulgaris Levyns. S. Africa, Australia.
C. zeyheri Fenzl ex Harvey. S. Africa.

104. **LEPTINELLA** Cass. in *Bull. Sci. Soc. philom. Paris* **1822**: 127 (1822). Type species: *L. scariosa* (Cass.) Franchet (Lloyd, 1972*a*).

Perennial or facultative annual herbs, prostrate or rarely suberect. Leaves alternate or opposite, pinnatisect. Capitula solitary, pedunculate, axillary, discoid or disciform, with varying proportions of pistillate and staminate florets or unisexual or both. Receptacle flat or conical, epaleate. Outer, female florets fertile, in one to several rows, tubular, conical to cylindrical, inflated with a hollow space between the outer surface and an inner layer closely surrounding the style. Central florets female-sterile, functionally staminate; corolla 4-lobed. Cypselas dorsiventrally flattened or more often thick and convex on the dorsal surface at least, glabrous or rarely with tapering uniseriate hairs on the margins. Pappus absent.

DISTRIBUTION. New Guinea, Australia, New Zealand and its subantarctic islands and one species in South America and the Falkland Islands. – 33 spp.

Until recently resurrected by Lloyd & Webb (1987), *Leptinella* has been included in the genus *Cotula* since being relegated to it as an infrageneric section by Hooker (1864). Lloyd (1972*a,b*) divided *Cotula* into three sections: sect. *Cotula*, sect. *Strongylosperma* (Less.) Benth. and sect. *Leptinella* (Cass.) Benth. Although Lloyd & Webb (1987) consider that it is very likely that the three sections form a monophyletic group we think so only with the addition of the genus *Soliva*. As described below *Soliva* is related to sect. *Strongylosperma* and these two groups together with *Cotula* and *Leptinella* are most likely a monophyletic group. Lloyd & Webb (1987) argue that because *Leptinella* is defined by the three distinctive autapomorphies it should be recognized as a genus in its own right. All species of *Leptinella* share the same habit, the same peculiar female floret morphology and all species examined so far have a chromosome number of x=13. Furthermore, the distribution is clearly West Pacific occurring in New Guinea, southeast Australia, New Zealand and the subantarctic islands. For the New Zealand species and the New Guinea species the treatments by Lloyd (1972*a*) and van Royen & Lloyd (1975), respectively, are available.

L. albida (D. Lloyd) D. Lloyd & C. Webb (*Cotula sericea* (Kirk) Cockayne & Allan). New Zealand.
**L. altilitoralis* (P. Royen & D. Lloyd) D. Lloyd & C. Webb. New Guinea.
L. atrata (Hook. f.) D. Lloyd & C. Webb. New Zealand.
L. calcarea (D. Lloyd) D. Lloyd & C. Webb. New Zealand.
L. dendyi (Cockayne) D. Lloyd & C. Webb. New Zealand.
L. dioica Hook. f. New Zealand.
L. dispersa (D. Lloyd) D. Lloyd & C. Webb. New Zealand.
**L. drummondii* (Benth.) D. Lloyd & C. Webb. Australia.
L. featherstonii F. Muell. (*Cotula renwickii* Cockayne). New Zealand.
**L. filicula* (Hook. f.) Hook. f. Australia (Tasmania).
L. filiformis (Hook. f.) D. Lloyd & C. Webb. New Zealand.
L. goyenii (Petrie) D. Lloyd & C. Webb. New Zealand.
L. intermedia (D. Lloyd) D. Lloyd & C. Webb. New Zealand.
L. lanata Hook. f. New Zealand.
L. leptoloba (Mattf.) D. Lloyd & C. Webb. New Guinea.
L. longipes Hook. f. Australia.
L. maniototo (Petrie) D. Lloyd & C. Webb. New Zealand.
L. minor Hook. f. (*Cotula haastii* Kirk). New Zealand
L. nana (D. Lloyd) D. Lloyd & C. Webb. New Zealand.
L. pectinata (Hook. f.) D. Lloyd & C. Webb (*Cotula monticola* Simpson, *C. villosa* Simpson, *C. willcoxii* Cheeseman). New Zealand.
L. plumosa Hook. f. New Zealand.
L. potentillina (F. Muell.) Druce. New Zealand.
L. pusilla Hook. f. (*Cotula perpusilla* Hook. f.). New Zealand.
L. pyrethrifolia (Hook. f.) D. Lloyd & C. Webb (*Cotula linearifolia* Cheeseman). New Zealand.
**L. reptans* (Benth.) D. Lloyd & C. Webb. Australia.
L. rotundata (Cheeseman) D. Lloyd & C. Webb. New Zealand.
**L. sarawaketensis* (P. Royen & D. Lloyd) D. Lloyd & C. Webb. New Guinea.
L. scariosa (Cass.) Franchet. Southern S. America, Australia.
L. serrulata (D. Lloyd) D. Lloyd & C. Webb. New Zealand.
L. squalida Hook. f. New Zealand.
L. tenella (Cunn.) D. Lloyd & C. Webb (*Cotula membranacea* D. Lloyd). New Zealand.
L. traillii (Kirk) D. Lloyd & C. Webb. New Zealand.
L. wilhelminensis (P. Royen) D. Lloyd & C. Webb. New Guinea.

105. **SOLIVA** Ruíz Lopez & Pavon, *Fl. peruv. prodr.*: 113 (1794). Type species: *S. sessilis* Ruíz Lopez & Pavon – *Gymnostyles* Juss.

Annual herbs. Leaves alternate, pinnatisect. Capitula solitary, sessile in the leaf axils, disciform. Receptacle convex or conical, epaleate. Outer florets female, fertile, in several rows; tube and limb absent; style persistent and spinescent in fruit. Central florets functionally male (style-branches fused); corolla 3- or 4-lobed. Cypselas dorsiventrally flattened, with 2 lateral vascular strands, laterally winged; wings sometimes projected to apical teeth, sometimes transversely rugose to sulcate. Pappus absent.

DISTRIBUTION. Mainly S. America but also in Australia and N. America, two species widespread as weeds (*S. sessilis*, *S. stolonifera*). – 8 spp.

Soliva with *Gymnostyles* included is a well-defined monophyletic group characterized by the sessile capitula with female florets in several rows and functionally male central florets, and the persistent and more or less spinescent style. *Gymnostyles*, with the single species *G. stolonifera* cannot be retained (e.g. Tutin in Tutin et al., 1976). It differs from *Soliva* by its villous cypselas with transversely sulcate wings. Similar pubescent cypselas but with less extremely sulcate wings occur in some species of *Soliva* (*S. anthemifolia*) (Webb, 1986). The alternative would be to transfer *S. anthemifolia* and related species to *Gymnostyles* but it seems quite unnecessary with two small, very similar and closely related genera rather than a single well-defined one. This solution is adopted also by Cabrera (1949) in his revision of the genus.

S. anthemifolia R. Br.
**S. macrocephala* Cabrera
**S. mutisii* Kunth
**S. neglecta* Cabrera
S. sessilis Ruíz Lopez & Pavon (*S. pterosperma* (Juss.) Less.)
S. stolonifera (Brot.) R. Br. ex G. Don in Loudon (*Gymnostyles stolonifera* (Brot.) Tutin)
**S. triniifolia* Griseb.
S. valdiviana Philippi

106. **SCHISTOSTEPHIUM** Less. in *Syn. gen. Compos.*: 251 (1832). Type species: *S. flabelliforme* Less. – *Peyrousea* DC.

Shrublets or half-shrubs. Leaves alternate, pinnatisect, lobed, dentate or occasionally entire. Capitula corymbose, occasionally solitary, disciform or discoid. Receptacle convex or conical, epaleate. Outer female florets tubular without limb, fertile, generally stalked. Central corolla 4-lobed. Cypselas dorsiventrally flattened, with 2 lateral (occasionally 3 or 4) vascular strands, sometimes with myxogenic cells. Pappus absent.

DISTRIBUTION. S. Africa from the E. Cape, Natal, and Transvaal to Mocambique and Zimbabwe. – 12 spp.

Schistostephium is distinguished from the related genus *Hippia* by its 4-lobed corolla and perfect disc-florets. It was revised by Hutchinson (1916*b*). The monotypic *Peyrousea*, revised by Bremer (1977, 1978), is very close to some species within *Schistostephium*, which appears to be paraphyletic with *Peyrousea* excluded. Hence we have merged the two genera.

S. crataegifolium (DC.) Fenzl ex Harvey (*S. villosum* Hutch.)
S. dactyliferum Hutch.
S. flabelliforme Less.
S. griseum (Harvey) Hutch.
S. heptalobum (DC.) Oliver & Hiern (*S. saxicola* Hutch.)
S. hippiifolium (DC.) Hutch.
S. mollissimum Hutch.
S. oxylobum S. Moore
**S. rogersii* Hutch.
S. rotundifolium (DC.) Fenzl ex Harvey
S. scandens Hutch.
S. umbellatum (L. f.) Bremer & Humphries, **comb. nov.** Basionym: *Cotula umbellata* L. f., *Suppl. pl.*: 378 (1781) (*Peyrousea umbellata* (L. f.) Fourc.).

107. **HIPPIA** L., *Mant. pl.* **2:** 158 (1771). Type species: *H. frutescens* (L.) L.

Shrublets or half-shrubs. Leaves alternate, pinnatisect, lobed, dentate or occasionally entire. Capitula corymbose, occasionally solitary, disciform. Receptacle convex or conical, epaleate. Outer female florets tubular without limb, fertile; tube much reduced. Central florets functionally male (style-branches fused); corolla 5-lobed, sometimes zygomorphic with 2 larger and 3 smaller lobes. Cypselas dorsiventrally flattened, with 2 lateral vascular strands, generally laterally winged. Pappus absent.

DISTRIBUTION. S. Africa in the Cape. – 8 spp.

Hippia is traditionally distinguished by its functionally male central florets. It also differs by its 5-lobed corolla from the related *Cotula* and *Schistostephium* with 4-lobed corollas. In these two characters *Hippia* agrees with *Eriocephalus* but the two genera are otherwise very different. *Hippia* is generally treated together with *Schistostephium*, while *Eriocephalus* is considered isolated. For reasons of parsimony *Eriocephalus* is placed here as the sister group of *Hippia*.

Hippia was revised by Hutchinson (1918). *H. montana* and *H. hutchinsonii* were later described by Compton (1940) and Merxmüller (Suessenguth and Merxmüller, 1951), respectively.

H. bolusae Hutch.
H. frutescens (L.) L.
H. hirsuta DC.
**H. hutchinsonii* Merxm.
H. integrifolia Less.
**H. montana* Compton
H. pilosa (P. J. Bergius) Druce
**H. trilobata* Hutch.

108. **ERIOCEPHALUS** L., *Sp. pl.*: 926 (1753). Type species: *E. africanus* L.

Shrubs, sometimes spinescent. Leaves alternate, sometimes opposite, often fascicled, variously lobed or entire, mostly ericoid. Capitula corymbose (pseudoumbellate or pseudoracemose) or close together or occasionally solitary, radiate or disciform. Involucral bracts in 2 unequal series; one outer row of pubescent to glabrescent, scarious bracts and one inner row of generally densely villous, often connate bracts. Receptacle paleate; paleae generally villous. Ray or outer female florets fertile; limb white or mauve, short and wide, or absent. Disc florets functionally male (style-branches fused); corolla 5-lobed, yellow or mauve. Cypselas dorsiventrally flattened, with 2 lateral ribs with vascular strands. Pappus absent. Dehydrofalcarinone and dehydrofalcarinol present.

DISTRIBUTION. S. Africa mainly in the Cape but also in Namibia. – 26 spp.

Eriocephalus is one of the most distinct and specialized genera in the tribe. The flattened fruits indicate a relationship with *Cotula* and its South African relatives *Hippia* and *Schistostephium* or possibly with *Achillea* and its relatives. It is here placed with the former group, since it agrees with *Cotula* in chemistry. Within the *Cotula* group *Eriocephalus* is most parsimoniously placed as sister group of *Hippia*, despite that *Eriocephalus* seems very different.

The list of species is taken from Harvey (1865) with species

described later added (e.g. Nordenstam, 1964). For species occurring in Namibia Merxmüller (1967) should be consulted. The genus is presently under revision at Windhoek in Namibia.

E. africanus L.
E. aromaticus C. A. Smith
E. aspalathoides DC.
E. capitellatus DC.
E. dinteri S. Moore
E. ericoides (L. f.) Druce (*E. glaber* Thunb.)
E. eximius DC.
**E. kingesii* Merxm. & Eberle
E. macroglossus B. Nord.
E. microcephalus DC.
**E. pauperrimus* Merxm. & Eberle
E. petrophiloides DC.
E. pinnatus O. Hoffm.
**E. pteronioides* DC.
E. pubescens DC.
E. punctulatus DC.
E. racemosus L.
E. scariosissimus S. Moore
E. scariosus DC.
E. septulifer DC.
E. sericeus Gaudich. ex DC.
E. spinescens Burch.
**E. tenuipes* C. A. Smith
E. tuberculosus DC.
E. umbellulatus Cass.
E. xerophilus Schltr

EXCLUDED GENERA

Potential future transfers, where known, are suggested in parenthesis.

Abrotanella Cass. (Senecioneae – Blennospermatinae Less.)
Baileya A. Gray (Heliantheae; near *Psilostrophe* DC.)
Centipeda Lour (Astereae)
Ceratogyne Turcz. (Astereae)
Chondropyxis D. Cooke (Gnaphalieae)
Dimorphocoma F. Muell. & Tate (Astereae)
Elachanthus F. Muell. (Astereae)
Formania W. W. Smith & Small (Astereae)
Ischnea F. Muell. (Senecioneae – Blennospermatinae Less.)
Isoetopsis Turcz. (Gnaphalieae)
Lepidostephium Oliver (Gnaphalieae – Athrixiinae)
Leucampyx A. Gray (Heliantheae; = *Hymenopappus* L' Hérit.)
Oedera L. (Gnaphalieae, near *Relhania* L' Hérit. emend Anderb. & Bremer, and *Leysera* L.)
Plagiocheilus Arn. ex DC. (Astereae; near *Lagenophora* Cass. & *Solenogyne* Cass.).
Pseudocadiscus Lisowski (Senecioneae; = *Stenops* B. Nord.).

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INDEX

Accepted names are in roman, synonyms in *italics*, new names and principal references in **bold**.